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PHILADELPHIA

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THE BUTTERFLY TYPES OF HENRY SKINNER AND CO-AUTHORS IN THE ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA

(LEPIDOPTERA: PAPILIONOIDEA AND HESPERIOIDEA)

BY NICHOLAS W. GILLHAM

Harvard University, Cambridge, Massachusetts

AND

PAUL R. EHRLICH

University of Kansas, Lawrence, Kansas

In the last few years the authors have had the opportunity, on numerous occasions, to examine the Lepidoptera collection of the Academy of Natural Sciences of Philadelphia. During the time we spent there we compiled this list of types of species described by Henry Skinner, since by far the majority of his types are housed in the Academy collections.[1] In addition, we have included the "types" that we found for names proposed by Skinner together with his several co-authors.

In many cases it will be noted that we have listed holotype and/or allotype in quotes. We have done this in order to avoid the possibility of mistakenly designating lectotypes and perhaps even neotypes. In the majority of cases these specimens are almost undoubtedly the original types, but in a few cases they are very dubiously so. Only when we are positive that a specimen is an authentic type have we omitted these quotes.

A few remarks on some of the headings used in the text should be made although they are in general self-explanatory. "Type No." refers to the number on the type label of the specimen; this is the Academy type number. The heading, "Data on Type," pertains to the date and locality labels on the specimen as well as any additional information of importance. Several sentences from the original description concerning the place where the types were collected are quoted under the heading, "Type Locality."

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[1] Type specimens for the following Skinner names were not located by us: *Colias philodice* var. *melanic* Skinner, *Colias philodice* var. *albinic* Skinner, *Pamphila streckeri* Skinner, and *Pamphila yehl* Skinner.

Our arrangement of species, genera, and other categories in this paper is based primarily on McDunnough's checklist (1938) and to a lesser degree on Klots (1951) and Evans (1951, 1952).

We would like to acknowledge the valuable aid given us by Dr. F. H. Rindge of the American Museum of Natural History in New York, Mr. James A. G. Rehn of the Academy, and by Mr. Harry Clench of the Carnegie Museum in Pittsburgh in completing this paper.

PAPILIONOIDEA

PAPILIONIDAE

PAPILIO Linnaeus

(1) **Papilio phflenor hirsuta** Skinner

Type No.: 7028.

Original Description: 1908, Ent. News 19:149.

Data on Type: Holotype male and allotype, " California."

Type Locality: " Male and female from Plumas County, California, 9500 feet elevation. Received from Mr. George Franck."

(2) **Papilio asterias** var. ♀ **alunata** Skinner and Aaron

Type No.: 7012.

Original Description: 1889, Canadian Ent., 21:127.

Data on Type: " Holotype " female, " Fairmount Park, Phila."

Type Locality: " Although the type specimen of *alunata* has no locality label on it, we have good reason to believe it to be from this region. The specimen in Dr. Skinner's collection was taken in Fairmount Park."

Remarks: We wonder if the specimen labeled " holotype " in the Academy of Natural Sciences collection is the true type, after reading the original description.

(3) **Papilio polyxenes** var. **curvifascia** Skinner

Type No.: 7026.

Original Description: 1902, Ent. News, 13:183.

Data on Type: " Holotype " male, " Rincon, N. Mex.," and allotype, " Rincon, N. Mex., VI/1."

Type Locality: " Described from 6 males and 1 female from Rincon, New Mexico, taken June 1, 1898, and kindly submitted for examination by Mr. Geo. Franck, of Brooklyn, N. Y."

(4) **Papilio rutulus** var. **arcticus** Skinner

Type No.: 7027.

Original Description: 1906, Ent. News, 17:379.

Data on Type: "Holotype" male, "Eagle, Alaska, 6/15/01"; the allotype has not been located.

Type Locality: "Described from six males and one female. Five males and one female from Eagle City, Alaska, June 1st to 15th. One male from Athabasca River, Canada."

PARNASSIUS Latreille

(5) **Parnassius immaculata** Skinner

Type No.: 7025.

Original Description: 1911, Ent. News, 22:108.

Data on Type: Holotype male, "Yel. Park, Wyo., collected by W. Judson Coxey."

Type Locality: "Described from one specimen, taken at the Old Faithful Geyser, Yellowstone Park, Wyoming, by Mr. W. Judson Coxey. . . ."

PIERIDAE

ANTHOCHARIS Boisduval

(6) **Anthocharis genutia** var. **flavida** Skinner

Type No.: 7029.

Original Description: 1917, Ent. News, 28:438.

Data on Type: "Holotype" male and "allotype," "Savannah, Ga., III-12-17, W. J. Coxey."

Type Locality: "On March 12 of the present year [1917] Mr. W. J. Coxey caught two pairs [of *A. genutia*] at Savannah, Georgia, ..."

(7) **Anthocharis sara** var. **browningi** Skinner

Type No.: 903.

Original Description: 1904? or 1906?, A Synonymic Catalogue of North American Rhophalocera, Supplement 1, page 22.

Data on Type: The data on the "holotype" male is, "Salt Lake City, Utah, V/9"; "allotype" same except, "VI/6."

Type Locality: "I have large series from Brightons, Utah, and City Creek Canyon, near Salt Lake City."

COLIAS Fabricius

(8) **Colias hecla** var. **pallida** Skinner (?)

Type No.: 7030.

Original Description: 1892, Ent. News, 3, plate 2, fig. 4, and the legend on the page facing the plate.

Data on Type: The data on the " holotype " female is, " Greenland, 1891."

Type Locality: " The specimens are all from the west coast of Greenland and were taken at three principal localities: McCormick Bay, Herbert Island, and Disco." We have quoted this statement from the Proceedings of the Academy of Natural Sciences of Philadelphia, 1892, 44:156.

Remarks: The method by which *pallida* was described is very confusing. It is figured on the above mentioned plate in the Entomological News along with several other butterflies and moths as an example of a method of photography. The page facing the plate gives names for all the figured specimens saying that the ones coming from Greenland will be discussed in a later paper. The paper referred to, by Skinner and Levi Mengel, came out in the Proceedings of the Academy of Natural Sciences of Philadelphia, 1892, 44:156 and in it *pallida* is fully described as a new variety. However, the photograph and legend in the Ent. News have several months priority over this article. The problem is made more confusing by the fact that in all the past references we can find the name is credited to Skinner despite the fact that he is not listed in the article in the Ent. News as being the author of the plate or its legend. Since this paper is not intended to make nomenclatorial changes we have credited the name to Skinner, following the example of other authors, wishing merely to point out that the correct authorship of the name is open to question. In this connection our remarks on *Argynnis chariclea* var. *gronlandica* should also be noted.

PIERIS Schrank

(9) **Pieris rapae** var. **immaculata** Skinner and Aaron

Type No.: 902.

Original Description: 1889, Canadian Ent., 21:128.

Data on Type: " Holotype " male, " Penn."

Type Locality: " Described from 5 specimens in the collection of Dr. Skinner and E. M. Aaron."

SATYRIDAE

ENODIA Huebner

(10) **Debis creola** Skinner

Type No.: 7039.

Original Description: 1897, Ent. News, 8:236.

Data on Type: The data on the " holotype " male is, " Opelousas, Louisiana, VII/3/97, Skinner."

Type Locality: " My specimens were kindly sent to me by Mr. G. R. Pilate, who captured them at Opelousas, La. on July 3d, present year. Dr. Strecker's specimen came from Texas."

Remarks: The " allotype " has been examined by the authors and was found to be a female of *Enodia portlandia* Fabricius.

OENEIS Huebner

(11) **Chionobas alberta** var. **oslari** Skinner

Type No.: 7040.

Original Description: 1911, Ent. News, 22:220.

Data on Type: The data on both the " holotype " male and " allotype " is, " Deer Creek Canyon, Colo., IX-25-09, Oslar."

Type Locality: ". . . described from two males, two females taken by E. J. Oslar in Deer Creek Canyon, Colorado, September 25, 1909."

EREBIA Dalman

(12) **Erebia sine-ocellata** Skinner

Type No.: 7042.

Original Description: 1889, Canadian Ent., 21:239.

Data on Type: " Holotype " male from, " Fort Qu'appele, Sask., Canada, Mrs. Rose."

Type Locality: " Described from two specimens, one from Ft. Qu'appelle, and other in coll. Am. Ent. Soc., locality unknown."

NYMPHALIDAE

SPEYERIA Scudder

(13) **Argynnis apacheana** Skinner

Type No.: 7031.

Original Description: 1918, Ent. News, 29:67.

Data on Type: The " holotype " male is from, " Arizona, collector Skinner."

Type Locality: Arizona.

Remarks: The process by which *apacheana* was named is very unusual. We now submit a quotation from Skinner's original description which is partly explanatory.

" I propose the name *apacheana* for the species of *Argynnis* described and figured by Mr. W. H. Edwards in Volume I of his Butterflies of North America, plate IV of *Argynnis,* figures 1, 2, ♂, 3, 4, ♀, under the name *nokomis."*

Skinner, in his original description, indicates that *apacheana* comes from Arizona, but nowhere in his paper does he mention a specimen that he designates as type. We would think that the specimen labeled as type in the Academy collection is of rather doubtful authenticity to say the least, and in fact one wonders if there is a type at all. However, dos Passos and Grey in their Catalogue of Speyeria (1947) consider the type locality as Arizona and the type as being deposited in the Academy. Therefore, following their example, we have considered that there was a type specimen of *apacheana,* and that the above mentioned specimen is probably it, although we list it as such only provisionally and definitely not absolutely.

(14) **Argynnis sakuntala** Skinner

Type No.: 7035.

Original Description: 1911, Ent. News, 22:108.

Data on Type: Lectotype male from, " Kaslo, B. C., 7-VII-1890, Cockle," and the " allotype," " Alberta, N.W.T.", and also on the " allotype " is the label, " Butterfly Book pl. 56 fig. 4."

Type Locality: " Described from 4 males, and 1 female. . . . Habitat Ainsworth, B. C., Aug. 13, 1903, Rev. G. H. Findley; Kaslo, B. C. July 7, 1890, J. W. Cockle; Laggan, Alberta, T. E. Bean. . . . Type locality, Kaslo, B. C."

Remarks: The male specimen mentioned under the heading " Data on Type " was designated the lectotype of the species by dos Passos and Grey (1947) on page 21 of their, " Catalogue of Speyeria."

(15) **Argynnis snyderi** Skinner

Type No.: 7033.

Original Description: 1897, Canadian Ent., 29:154.

Data on Type: Lectotype male, " Salt Lake, Ut., 6/23/95 " and on the " allotype " is, " Ogden, Utah, 7/16/95."

Type Locality: " I have specimens from Salt Lake City, Utah, taken June 23rd, 1895 and a female from Ogden, July 6th, 1895. All were taken by Prof. A. J. Snyder. . . ."

Remarks: The male specimen mentioned under the heading " Data on Type " was designated the lectotype by dos Passos and Grey, l.c., page 11.

(16) **Argynnis californica** Skinner

Type No.: 7034.

Original Description: 1917, Ent. News, 28:328.

Data on Type: The data on the " holotype " male is, " Alma, Cala.," and on the " allotype " is, " Cal."

Type Locality: " Described from 15 specimens from California, the type and paratypes were taken by Mr. J. G. Grundel at Alma, Santa Clara County."

(17) **Argynnis platina** Skinner

Type No.: 7032.

Original Description: 1897, Canadian Ent., 29:154.

Data on Type: " Holotype " male and " allotype," " Ogden, 7/18/95."

Type Locality: " Described from specimens taken at Ogden, Utah, between July 18th and 24th, and Beaver Canon, Idaho, at nearly same dates. From Prof. A. J. Snyder."

(18) **Argynnis utahensis** Skinner

Type No.: 7036.

Original Description: 1919, Ent. News, 30:216.

Data on Type: The data on the holotype male is, " Cy. Creek Cañon, 7/6, H. Skinner," and on the allotype is, " Silver Lake, Ut., 7/12, H. Skinner."

Type Locality: " The type was taken by the writer in City Creek Canyon, Salt Lake City, Utah, July 6th, and the allotype at Silver Lake, Brightons, Utah, July 12."

BOLORIA Moore

(19) **Argynnis laurenti** Skinner

Type No.: 7024.

Original Description: 1913, Ent. News, 24:450.

Data on Type: " Holotype " male, " Silver Lake, Ut., 7/11, H. Skinner," and the " allotype," " Silver Lake, Ut., 7/10, H. Skinner."

Type Locality: " Described from 8 specimens taken by Mr. Philip Laurent and the author, at Silver Lake [Brightons], Utah, July 10th to 14th, 1899."

(20) **Argynnis chariclea** var. **" gronlandica "** Skinner (?)

Type No.: 7781.

Original Description: 1892, Ent. News, 3:plate 2, figures 9 & 10, and the page facing plate 2.

Data on Type: " Holotype " female, " Greenland," and the " allotype," " McCormick Bay, Greenl'd, 7/36."

Type Locality: " The specimens are all from the West coast of Greenland taken at three principal localities: McCormick Bay, Herbert Island, and Disco. They were captured by Levi W. Mengel, and Dr. W. E. Hugh[e]s." This is the same quote from the Skinner & Mengel paper, l.c., given under *Colias hecla* var *pallida* Skinner. It should be noted that this quote is at the beginning of the paper and applies to all the species mentioned in the remainder of the paper.

Remarks: This species was described in the same manner as *Colias hecla* var. *pallida.* The original description consists of figures 9 and 10 on plate 2 of the above mentioned volume of the Entomological News plus the legend of the plate on the facing page. It is interesting to note, however, that the name " *gronlandica* " is not applied to these specimens in the Skinner and Mengel paper, l.c., a different name, proposed by an earlier author, being used. There is, nevertheless, the same problem concerning the authorship of this name as there was with " *pallida* ". This problem being that we can find no place where an author's name is given for the plate or its legend in which the name " *gronlandica* " is proposed. The name has usually been credited to Skinner by later authors but we feel that this may well be a mistake since, although the article may very likely have been written

by Skinner, there is no author given. The same sort of reasoning may be applied to the name "*pallida*" except that in this case Skinner and Mengel, l.c., fully redescribe it as a new variety. Therefore, "*pallida*" Skinner should probably be *pallida* Skinner & Mengel. However, as previously remarked, this is not a revisionary paper and since this is so we wish merely to establish the fact that these names are questionably referable to Skinner and should be more fully investigated.

EUPHYDRYAS Scudder

(21) **Melitaea maria** Skinner

Type No.: 7018.

Original Description: 1899, Canadian Ent., 31:12.

Data on Type: "Holotype" male, "Park Cy., Ut., VI/26."

Type Locality: "Described from a number of specimens taken at Park City, Utah, June 26th, 1895, by Prof. A. J. Snyder, ..."

(22) **Melitaea beani** Skinner

Type No.: 7016.

Original Description: 1897, Canadian Ent., 29:155.

Data on Type: "Holotype" male, "Alberta, Bean," and the "allotype," "Laggan, Alberta."

Type Locality: "I propose this name [*beani*] for the Alpine form of *anicia* from the high elevation near Laggan, Alberta, . . ."

(23) **Melitaea glacialis** Skinner

Type No.: 7022.

Original Description: 1921, Ent. News. 32:89.

Data on Type: Holotype female, "Glacier Nat. Pk., VII-15-20, Mont., Annette F. Braun."

Type Locality: "One specimen, taken at Two Medicine Lake, Glacier National Park, Montana, July 15, 1920, by Miss Annette F. Braun. . . ."

MELITAEA Fabricius

(24) **Melitaea neumoegeni** Skinner

Type No.: 7019.

Original Description: 1895, Ent. News, 6:113.

Data on Type: "Holotype" male and "allotype," "Utah, collect. Skinner."

Type Locality: " Described from three specimens in my own collection and from several in the late Mr. Neumoegen's. From Utah."

(25) **Melitaea damoetas** Skinner

Type No.: 7021.

Original Description: 1902, Ent. News, 13:304.

Data on Type: " Holotype " male, " Wms. Riv. Ran., Col., VIII-9-02, Coll. A. J. Snyder," and the following label is also present, " Butterfly Book, Pl. 56, fig. 13."

Type Locality: " Described from 4 specimens, from Colorado as follows: one from South Park, VIII.15.02, John and Hurd Comstock; two from Prof. A. J. Snyder, Williams River Range, VIII.9.02, and Hall Valley, VII.21.02; one from E. J. Oslar."

PHYCIODES Huebner

(26) **Phyciodes barnesi** Skinner

Type No.: 7037.

Original Description: 1897, Canadian Ent., 29:155.

Data on Type: " Holotype " male from, " Glenwood Spgs., Col., June 1-7."

Type Locality: " Specimens were taken at Glenwood Springs, Colo., May 8th to 15th, and June 1st to 7th, by Dr. Wm. Barnes, in whose collection are many co-types."

(27) **Melitaea arida** Skinner

Type No.: 7020.

Original Description: 1917, Ent. News, 28:328.

Data on Type: " Holotype " male, " Cochise Co., Ariz., May."

Type Locality: " Type and paratype. Two specimens marked Cochise Co. Arizona, May. Received from Mr. F. Haimbach without more definite locality."

ANTHANASSA Scudder

(28) **Eresia texana** subsp. **seminole** Skinner

Type No.: 7023.

Original Description: 1911, Ent. News, 22:412.

Data on Type: " Holotype " male and " allotype " from, " Bainbridge, Ga., IX/17-X/19-10, J. C. Bradley."

Type Locality: " Described from 2 specimens . . . in the collection of Academy of Natural Sciences of Philadelphia and a number of paratypes in the collection of the Georgia State Board of Entomology at Atlanta. The specimens were taken by Prof. J. C. Bradley, at Bainbridge, Georgia, Sept. 17th."

ANARTIA Huebner

(29) **Anartia dominica** Skinner

Type No.: 7051.

Original Description: 1889, Trans. American Ent. Soc., 16:86.

Data on Type: " Holotype " male, " Hayti, Dr. Abbot," and the " allotype," " San Domingo, Frazar, 1883."

Type Locality: " Described from five specimens, four males and one female. Two were caught at Samana Bay, by Dr. W. C. Abbott, and are in the collection of the Am. Ent. Soc. Two were presented to me by my friend, Mr. E. M. Aaron, and one received from Mr. A. G. Weeks, Jr.; all are from Hayti."

MYSCELIA Doubleday

(30) **Myscelia streckeri** Skinner

Type No.: 7176.

Original Description: 1889, Trans. American Ent. Soc., 16:87.

Data on Type: " Holotype " male and " allotype," " L. Cal."

Type Locality: " Described from five specimens from Lower California through the kindness of Mr. A. G. Weeks, Jr."

CATAGRAMMA Bates

(31) **Catagramma oberthuri** Skinner

Type No.: 7050.

Original Description: 1916, Ent. News, 27:307.

Data on Type: " Holotype," " Rio Madeira, Brazil, S. A., Smith, 8° 45′ S. 63° 54′ W."

Type Locality: " Described from two males from the Rio Madeira, Brazil, 8 deg. 45 min. South, 63 deg. 54 min. West."

ASTEROCAMPA Rober

(32) **Chlorippe clyton** var. **texana** Skinner

Type No.: 7038.

Original Description: 1911, Trans. American Ent. Soc., 37:214.

Data on Type: Holotype male, "Round Mt., Tex., 7/31/95," and on the "allotype," "Texas, S. F. A., 1884."

Type Locality: "The male type was taken at Round Mountain, Texas, July 31, 1895 by F. G. Schaupp, and the female near Corpus Christi by S. F. Aaron (see Papilio 4, 179, 1884)."

RIODINIDAE

APODEMIA Felder & Felder

(33) **Lemonias palmeri** var. **marginalis** Skinner

Type No.: 7041.

Original Description: 1920, Ent. News, 31:175.

Data on Type: "Holotype" male and allotype, "Acme, Cal., VIII-8-1919, Hebard."

Type Locality: "Type male and paratypes male and female from Acme, California, August 8, 1919, (Morgan Hebard)."

MESOSEMIA Huebner

(34) **Mesosemia ramsdeni** Skinner

Type No.: 7067.

Original Description: 1912, Ent. News, 23:126.

Data on Type: Holotype male and allotype, "La Yberia, 20 miles west of Baracoa, Cuba, IX-18-09, C. T. Ramsden."

Type Locality: "From two specimens male and female, from La Yberia, twenty miles from Baracoa, Cuba, September 18th, 1909."

LYCEANIDAE

STRYMON Huebner

(35) **Thecla sarita** Skinner

Type No.: 7043.

Original Description: 1895, Ent. News, 6:112.

Data on Type: Holotype male, "New Braunfels, Comal Co., Tex."

Type Locality: "Described from one specimen, a ♂, received from Mr. F. Rauterberg, . . . from Comal County, Texas."

MITOURA Scudder

(36) **Thecla johnsoni** Skinner

Type No.: 7044.

Original Description: 1904, Ent. News, 15:298.

Data on Type: " Holotype " female, " Br. Cola.," and " allotype," " Seattle, Wash."

Type Locality: " The female bears a label British Columbia. . . . The male was sent to me by Prof. O. B. Johnson, of Seattle, Washington."

(37) **Thecla damon** var. **discoidalis** Skinner

Type No.: 7046.

Original Description: 1897, Canadian Ent., 29:156.

Data on Type: " Holotype " male, " Round Mt., Tex."

Type Locality: " Round Mountain, Blanco Co., Texas, February 10th and August 16th."

(38) **Thecla loki** Skinner

Type No.: 7045.

Original Description: 1907, Ent. News, 18:378.

Data on Type: " Holotype " male and " allotype," " Mt. Springs, San Diego County, Cal., VII-5-06."

Type Locality: " From 5 specimens taken by Mr. W. S. Wright at Mt. Springs, San Diego County, Cal., July 5, 1906."

PLEBEIUS Kluk

(39) **Lyceana chlorina** Skinner

Type No.: 7048.

Original Description: 1902, Ent. News, 13:15.

Data on Type: " Holotype " female, " Tehachapi, So. Cal., VII-6-95."

Type Locality: " Tehachapi, Cala. July 6th."

(40) **Lyceana neurona** Skinner

Type No.: 7047.

Original Description: 1902, Ent. News, 13:15.

Data on Type: " Holotype " female, " Doble, S. B. Co., Cala., Aug."

Type Locality: " Doble, San Bernardino County, Cal., August."

GLAUCOPSYCHE Scudder

(41) **Lyceana lygdamus** race **columbia** Skinner

Type No.: 7049.

Original Description: 1917, Ent. News, 28:213.

Data on Type: "Holotype" male and "allotype," "Port Columbia, Wash., IV-25-1916, J. C. Hopfinger."

Type Locality: "Described from type, male, from Port Columbia, Washington, April 25, 1916, and Paratypes, one male and two females with the same data. They were sent to me by Mr. J. C. Hopfinger."

HESPERIOIDEA

Pyrrhopyginae

PYRRHOPYGE Huebner

(42) **Pyrrhopyge viriditas** Skinner

Type No.: 7058.

Original Description: 1920, Ent. News, 31:132.

Data on Type: Holotype male, "San Pedro, Honduras."

Type Locality: "One specimen from San Pedro, Sula, Honduras."

(43) **Pyrrhopyge sangaris** Skinner

Type No.: 7057.

Original Description: 1921, Ent. News, 32:236.

Data on Type: "Holotype" male, "Hacienda Cincinnati, Sierra San Lorenzo, Magdalena, Columbia, 4500′ (R[ehn]), VII, 23, 1920."

Type Locality: ". . . taken at Hacienda Cincinnati, Sierra San Lorenzo, Magdalena, Columbia, July 23rd, 1920, ..."

MIMONIADES Huebner

(44) **Mimoniades amans** Skinner

Type No.: 7056.

Original Description: 1920, Ent. News, 31:132.

Data on Type: Holotype male, "Nieva, U. S. Col."

Type Locality: "One specimen from Nieva, United States of Columbia."

(45) **Mimoniades aemulus** Skinner

Type No.: 7054.

Original Description: 1920, Ent. News, 31:132.

Data on Type: Holotype male, " Ambato, Ecuador."
Type Locality: " One male specimen from Ambato, Ecuador."

PYRGINAE

POLYGONUS Huebner

(46) **Erycides amyntas arizonensis** Skinner

Type No.: 7073.
Original Description: 1911, Trans. American Ent. Soc., 37:209, figured on Plate 10.
Data on Type: " Holotype " male, " Florence, Ariz., IX-3, Biederman," " allotype " same except, " IX-18."
Type Locality: " Described from a number of specimens from Florence, Arizona, taken September 3rd (C. R. Biederman)."

PROTEIDES Huebner

(47) **Proteides jamaicensis** Skinner

Type No.: 7084.
Original Description: 1920, Ent. News, 31:133.
Data on Type: " Holotype " male, " Jamaica."
Type Locality: " The type and four other specimens from Jamaica."

URBANUS Huebner

(48) **Eudamus parvus** Skinner

Type No.: 7061.
Original Description: 1920, Ent. News, 31:134.
Data on Type: Holotype male, " St. Pierre, Martinique, XII-8-1911, J. M. Geddes," and " allotype," " Dominica, IX-23-1911, J. M. Geddes."
Type Locality: " The type locality (type male) is St. Pierre, Martinique (J. M. Geddes, Dec. 8th, 1911). Allotype from same locality. . . . "
Remarks: It seems, from the type locality stated in the original description, that the specimen labeled " allotype " in the A.N.S.P. collection is not the true allotype.

(49) **Eudamus protillus** var. **rauterbergi** Skinner

Type No.: 7062.
Original Description: 1895, Ent. News, 6:113.

Data on Type: Holotype male, "New Braunfels, Comal Co., Tex."

Type Locality: "One specimen from Mr. F. Rauterberg, who received it from Comal County, Texas."

CODATRACTUS Lindsey

(50) **Heteropia melon arizonensis** Skinner

Type No.: 7074.

Original Description: 1905, Ent. News, 16:232.

Data on Type: "Holotype" male, "Baboquivari Mts., Pima Co., Arizona, July 15 to 30, 1903, Coll. O. C. Poling," and a "paratype" with same data but with the additional label, "former type *arizonensis* Skin., J. W. C."

Type Locality: ". . . from the Baboquivaria [sic] Mts., Pima County, Arizona, July 15th to 30th, ..."

Remarks: Needless to say there is confusion here as to the true holotype of *arizonensis,* as is shown by the label on the so-called "paratype." Unfortunately we have not been able to determine which, if either, of these specimens is the holotype in reality.

ASTRAPTES Huebner

(51) **Thymele angustus** Skinner

Type No.: 7066.

Original Description: 1920, Ent. News, 31:133.

Data on Type: "Holotype" male, "San Domingo, Frazar, 1883."

Type Locality: "The type and two other specimens from San Domingo, West Indies."

(52) **Telegonus antiquus** Skinner

Type No.: 7065.

Original Description: 1920, Ent. News, 31:133.

Data on Type: "Holotype" male, "San Domingo, Frazar, 1883."

Type Locality: "The type and one other specimen from San Domingo, West Indies."

ACHALARUS Scudder

(53) **Eudamus coyote** Skinner

Type No.: 7075.

Original Description: 1892, Canadian Ent., 24:164.

Data on Type: " Holotype " male, " Texas, S.F.A., 1884."

Type Locality: " Described from five specimens from southern Texas in collection of author."

THORYBES Scudder

(54) **Eudamus pylades** var. **immaculata** Skinner

Type No.: 7175.

Original Description: 1911, Trans. American Ent. Soc. 37:177.

Data on Type: Holotype male, " Penn., 5-30-81."

Type Locality: " This specimen was taken at Philadelphia May 30th, ... "

(55) **Eudamus aemilea** Skinner

Type No.: 7076.

Original Description: 1893, Ent. News, 4:64.

Data on Type: " Holotype " male, " Ft. Klamath, Or., 6/6," also on the " holotype " is a label which reads as follows, " the true type is probably in Pittsburgh. See letter to Avinoff dated I/11/39. Also letter to dos Passos of Dec. 28, 1938." The data on the " allotype " is, " Ft. Klamath, Or."

Type Locality: " From five specimens, two males and three females, taken by Prof. Edw. T. Owen, at Fort Klamath, Oregon, ... "

Remarks: We have written to Mr. Harry Clench of the Carnegie Museum in Pittsburgh to find out whether or not the " true type " of *aemilea* is there as indicated by the label on the " holotype " in the Academy of Natural Sciences. We have also inquired about the letter to Dr. Avinoff mentioned on this label. Mr. Clench has been good enough to look at the *aemilea* in the Carnegie collection and has also examined the correspondence there. He writes us that it is very unlikely that any of the three specimens of *aemilea* there could be the holotype and also that he was unable to find any letter to Dr. Avinoff on the subject. Since we have not been able to contact Mr. dos Passos, whose name is also mentioned on the label

in reference to a second letter about the type of *aemilea,* we must leave the true location of the holotype open to question.

SALATIS Evans

(56) **Bungalotis canalis** Skinner

Type No.: 7063.

Original Description: 1920, Ent. News, 31:134.

Data on Type: Holotype male, "Gatun, Canal Zone, VII-30-1916, D. E. Harrower."

Type Locality: "The type is from Gatun, Canal Zone, Panama."

PORPHYROGENES Watson

(57) **Bungalotis immaculata** Skinner

Type No.: 7064.

Original Description: 1920, Ent. News, 31:133.

Data on Type: Holotype male, "Chanchamayo, Peru."

Type Locality: "Type from Chanchamayo, Peru."

PYRGUS Huebner

(58) **Pyrgus occidentalis** Skinner

Type No.: 7108.

Original Description: 1906, Ent. News, 17:96.

Data on Type: "Holotype" male, "San Antonio, Tex.," and the "allotype," "Alamogordo, N. M., IV-15-02."

Type Locality: "Prof. Snow sent me specimens from San Bernardino Ranch, Cochise Co., Arizona, August, and Brownsville, Texas."

Remarks: The specimens labeled "holotype" and "allotype" in the A.N.S.P. collection are almost certainly not the authentic types. There is quite obviously no correspondence between the data on the Academy specimens and the data that Skinner gives in his original description for the type locality. In addition, Mr. J. A. G. Rehn has informed us that the specimen labeled "allotype" was collected by H. L. Viereck and himself, whereas the original description states that the specimens were received from Prof. Snow.

ERYNNIS Schrank

(59) **Thanaos burgessi** Skinner

Type No.: 7089.

Original Description: 1914, Trans. American Ent. Soc., 40:203, with a figure of the male genitalia.

Data on Type: Holotype male, " Mt. Graham, Arizona, Morrison Col., 1882; Genitalic slide No. 1155," and the " allotype " with the same data except no slide label.

Type Locality: " Described from seven males and three females from Arizona. Two of these were taken in Arizona in 1883, by H. K. Morrison and the remainder by the same collector at Mt. Graham in that state in 1882. The single type, a male, in the collection of the Academy is from the latter locality."

(60) **Thanaos scudderi** Skinner

Type No.: 7088.

Original Description: 1914, Trans. American Ent. Soc., 40:215, male genitalia figured on page 216.

Data on Type: " Holotype " male, " Ariz.; Genitalia slide No. 1154; Micro Slide No. 394."

Type Locality: " Described from five specimens taken by H. K. Morrison, at Fort Grant, Arizona in 1883."

COGIA Butler

(61) **Eudamus outis** Skinner

Type No.: 7072.

Original Description: 1894, Ent. News, 5:332.

Data on Type: " Holotype " male, " Round Mt., Tex."

Type Locality: " Described from four males taken in Blanco County, Texas, Aug. 27, 1894."

Remarks: It should be mentioned that Round Mountain is in Blanco County, Texas.

EPHYRIADES Huebner

(62) **Ephyriades cubensis** Skinner

Type No.: 7085.

Original Description: 1913, Ent. News, 24:72.

Data on Type: Holotype female, " La Yberia 20 miles west of Baracoa, Cuba, 2000 ft. alt., IX-18-1909, C. T. Ramsden."

Type Locality: " Described from one specimen, from Mr. C. T. Ramsden, taken at La Yberia, twenty miles west of Baracoa, Cuba, September 18th, 1909. Altitude 2000 feet."

CYCLOGYPHA Mabille

(63) **Cyclogypha gundlachi** Skinner and Ramsden

Type No.: 7083.

Original Description: 1923, Proceedings of the Academy of Natural Sciences of Philadelphia, 75:314.

Data on Type: Holotype female, " Rio Seco, San Carlos Est., Guantanamo, Cuba, June 2 1914, coll. C. T. Ramsden."

Type Locality: " Guantanamo, Cuba, June 2, 1914 (Ramsden). One female (type) . . . . "

Hesperiinae

COPAEODES Edwards

(64) **Copaeodes chromis** Skinner

Type No.: 7100.

Original Description: 1919, Ent. News, 30:100.

Data on Type: Holotype male, " Colima, Mexico."

Type Locality: " Described from one male (?) specimen from Colima, Mexico."

HESPERIA Fabricius

(65) **Pamphila slossonae** Skinner

Type No.: 7765.

Original Description: 1890, Entomologica Americana, 6:138.

Data on Type: Holotype male and allotype from, " Fla."

Type Locality: " Described from one pair from Florida presented by Mrs. Slosson."

(66) **Pamphila pawnee** subsp. **montana** Skinner

Type No.: 7086.

Original Description: 1911, Ent. News, 22:413.

Data on Type: " Holotype " male, " Chaffee Co., Colo., 7500 ft, Bruce."

Type Locality: " Described from eleven specimens from Colorado, taken by David Bruce. Only two out of the lot have exact data; one says Chaffee County, 7500 feet alt., and the other Salida, May 21st, 7500 feet alt."

(67) **Pamphila sassacus** subsp. **dacotae** Skinner

Type No.: 7087.

Original Description: 1911, Ent. News, 22:412.

Data on Type: " Holotype " male, " Volga, P. C. Truman, VII-16," and " allotype," " S. Dak."

Type Locality: " Described from five specimens from Volga, South Dakota, and five from, Grinnel, Iowa. Type locality Volga. The insect flies in July and August (July 16-21, Aug. 24th)."

OCHLODES Scudder

(68) **Pamphila scudderi** Skinner

Type No.: 7097.

Original Description: 1899, Ent. News, 10:111.

Data on Type: Holotype male and allotype, " White R., Col., Jul. 24-Aug. 13."

Type Locality: " Described from a pair sent to me by Dr. S. H. Scudder who has a good series in his collection. They were taken on the White River, Colorado, between July 24th and August 13th."

POLITES Scudder

(69) **Pamphila alcina** Skinner

Type No.: 7090.

Original Description: 1893, Ent. News, 4:212.

Data on Type: " Holotype " male, " S.W. Colorado, Tolman, 1884."

Type Locality: " From three male specimens from Colorado; . . . ."

(70) **Pamphila sylvanoides** subsp. **utahensis** Skinner

Type No.: 7099.

Original Description: 1911, Ent. News, 22:413.

Data on Type: " Holotype " male, " Park City, Ut., VII-20," " allotype " same.

Type Locality: " Type locality, Park City, Utah, July 20th."

(71) **Pamphila mystic** subsp. **pallida** Skinner

Type No.: 7091.

Original Description: 1911, Ent. News, 22:412.

Data on Type: " Holotype " male, " S. Dak., 7/16," " allotype " same but, " 7/25."

Type Locality: " Described from a number of specimens of both sexes from Volga, South Dakota. Taken in July, from the 16th to the 25th."

(72) **Pamphila stigma** Skinner

Type No.: 7098.

Original Description: 1896, Canadian Ent., 28:188.

Data on Type: " Holotype " male, " S. N. Mex."

Type Locality: " From several specimens in the collection of the author and Dr. Herman Strecker, of Reading, Pa., from the southern border of New Mexico and S.—W. Texas."

POANES Scudder

(73) **Pamphila aaroni** Skinner

Type No.: 7093.

Original Description: 1890, Ent. News, 1:6.

Data on Type: " Holotype " male, " New Jersey."

Type Locality: Cape May, N. J. " . . . in company with *P. panoquin,* feeding on the flowers of *Statice limonium* var. *Americanum,* which grows in the salt meadows, ... "

(74) **Pamphila howardi** Skinner

Type No.: 7092.

Original Description: 1896, Canadian Ent., 28:187.

Data on Type: " Holotype " male and " allotype," " Florida."

Type Locality: " Described from eight specimens . . . . They are all from Florida; two being from Georgiana, on the Indian River; exact localities of others unknown."

(75) **Choranthus haitensis** Skinner

Type No.: 7094.

Original Description: 1920, Ent. News, 31:187.

Data on Type: Holotype male, " Port de Paix, Hayti, VII-27-17, W. L. Abbott."

Type Locality: " Described from a number of specimens from Haiti and San Domingo (Dr. W. L. Abbott) and the type male from Port de Paix, Haiti, VII, 27, 1917."

ATRYTONOPSIS Godman and Salvin

(76) **Pamphila vierecki** Skinner

Type No.: 7105.

Original Description: 1902, Ent. News, 13:213.

Data on Type: " Holotype " male, " Alamogordo, N. M., V/13 1902; Butterfly Book, pl. 54 fig. 3," and the " allotype," " Alamogordo, N. M., V/2 1902."

Type Locality: " Taken by Henry L. Viereck in Dry Canyon, Alamogordo, New Mexico, May 8th to 13th."

Remarks: Holland (1931) on the legend to the above mentioned plate in his book figures this specimen as a " paratype " rather than as the " holotype."

(77) **Pamphila margarita** Skinner

Type No.: 7106.

Original Description: 1913, Canadian Ent., 45:426.

Data on Type: " Holotype " male, " Jemez Mts., New Mex., VI-9-1913," and the " allotype " the same except that the date is, " V-31-1913."

Type Locality: " Described from a number of specimens of both sexes submitted by Mr. R. C. Williams . . . . They were captured at Jemez Springs, New Mexico, May 26th to June 9th, by Mr. John Woodgate."

PHEMIADES Huebner

(78) **Pyrrhocalles antiqua** form **orientis** Skinner

Type No.: 7104.

Original Description: 1920, Ent. News, 31:152.

Data on Type: Holotype male, " Guantanamo, Cuba, June 25 1910."

Type Locality: " The type is a male from Guantanamo (San Carlos ?), Cuba, taken July 25, 1910, for which I am indebted to Dr. Ramsden, ... "

AMBLYSCIRTES Scudder

(79) **Amblyscirtes celia** Skinner

Type No.: 7095.

Original Description: 1895, Ent. News, 6:113.

Data on Type: " Holotype " male, " New Braunfels, Tex.; Butterfly Book, Pl. LI Fig. 30."

Type Locality: " Described from specimens from Blanco, Comal and Nueces Counties, Texas."

Remarks: Holland, l.c., on the legend to the above mentioned plate in his book, figures this specimen as a " paratype " rather than as the " holotype."

(80) **Pamphila quinquemacula** Skinner

Type No.: 7107.

Original Description: 1911, Ent. News, 22:412.

Data on Type: Holotype male, " Las Cruces, N. Mex."

Type Locality: " From one specimen taken at Las Cruces, New Mexico, probably taken by Prof. T. D. A. Cockerell."

(81) **Pamphila carolina** Skinner

Type No.: 7096.

Original Description: 1892, Ent. News, 3:222.

Data on Type: " Holotype " male, " Hamlet, Richmond Co., N. C., VIII-23, F. M. Jones."

Type Locality: " . . . ' They were captured about one-half mile south of Hamlet, Richmond County, North Carolina, on the border of a small cane brake.' "

(82) **Pamphila oslari** Skinner

Type No.: 7101.

Original Description: 1899, Ent. News, 10:112.

Data on Type: " Holotype " male, " Chimney Gulch, Colo., 6/18."

Type Locality: " Described from four males taken in Chimney Gulch, Colorado, by Mr. E. J. Oslar on the 18th of June."

LERODEA Scudder

(83) **Lerodea neamathla** Skinner and Williams

Type No.: 7109.

Original Description: 1923, Trans. American Ent. Soc., 49:145.

Data on Type: Holotype male, " Fla.; Genitalic slide No. 1646," and the allotype, " Fla.; Genitalic slide No. 1648."

Type Locality: " Described from a male type and a female allotype, and two male and a female paratype. The specimens were taken in Central Florida in 1884 by H. K. Morrison, ... "

CALLIMORMUS Scudder

(84) **Callimormus dimidiatus** Skinner

Type No.: 7112.

Original Description: 1920, Ent. News, 31:134.

Data on Type: Holotype male, "Huigra, Ecuador, (S. N. Rhoads), Mar. 1911."

Type Locality: "Type, a male from Huigra, Ecuador, (S. N. Rhoads)."

PSEUDOSARBIA Berg

(85) **Pseudosarbia flavofasciata** Skinner

Type No.: 7055.

Original Description: 1921, Ent. News, 32:236.

Data on Type: "Holotype" male, "Chapada, Brazil, April, H. H. Smith."

Type Locality: "Described from two specimens taken by H. H. Smith in Chapada, Brazil."

PANOQUINA Hemming

(86) **Pamphila panoquinoides** Skinner

Type No.: 7103.

Original Description: 1891, Ent. News, 2:175.

Data on Type: "Holotype" male, "Key West, H. K. M., '85," and the "allotype," "Texas, S. F. A., 1884."

Type Locality: "Described from specimens from Key West, Fla. and Texas in the coll. of I. C. Martindale, Esq."

(87) **Pamphila errans** Skinner

Type No.: 7102.

Original Description: 1892, Ent. News, 3:174.

Data on Type: "Holotype" male, "Cal., Dyar."

Type Locality: "I have specimens from California received from Mr. H. G. Dyar and Dr. Blaisdell, and also specimens from Texas."

MEGATHYMIDAE

MEGATHYMUS Scudder

(88) **Megathymus yuccae** var. **navajo** Skinner

Type No.: 7052.

Original Description: 1911, Ent. News, 22:300; figured on plate 10.

Data on Type: " Holotype " male, " Mountain back of post; Fort Wingate, N. M., V-31-08, John Woodgate."

Type Locality: Skinner apparently had four specimens before him when he described *navajo*. " They came from Fort Wingate, New Mexico and were taken May 13th, 25th, 31st, and June 13th. One specimen's label says ' on mountain back of Fort'."

(89) **Aegiale streckeri** Skinner

Type No.: 7053.

Original Description: 1895, Canadian Ent., 27:179.

Data on Type: " Holotype " male, " Arizona, Morrison, 1883."

Type Locality: " This fine species is described from two males in my own collection; one is from Texas and the other probably from Arizona (the exact locality not being known in either case), and a pair in the collection of Dr. Herman Strecker, of Reading, Pa.; one of these is from Texas, and was collected by the late Jacob Boll, and the other from the San Juan reconnaissance made under the charge of Lieut. Ruffner in Colorado, in 1877."

(90) **Megathymus neumoegeni** subsp. **stephensi** Skinner

Type No.: 7060.

Original Description: 1912, Ent. News, 23:126.

Data on Type: " Holotype " female, " La Puerta, San Diego Co., Calif., 11-X-11," and the " allotype," " Eastern edge, San Diego Co., Cal., X-11-11."

Type Locality: " Type locality, La Puerta, eastern edge of San Diego County, California, October 11th 1911."

(91) **Megathymus polingi** Skinner

Type No.: 7059.

Original Description: 1905, Ent. News, 16:232.

Data on Type: Holotype male, " So. Arizona, Oct. 15-30," and allotype with the same data.

Type Locality: " Described from a male and female sent by Mr. O. C. Poling. The labels say So. Arizona, Oct. 15th to 30th. I suppose they were taken in the Baboquivari Mountains, Pima County."

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VENEREAL TRANSMISSION OF MITES BY WASPS, AND SOME EVOLUTIONARY PROBLEMS ARISING FROM THE REMARKABLE ASSOCIATION OF *ENSLINIELLA TRISETOSA* WITH THE WASP *ANCISTROCERUS ANTILOPE*. BIOLOGY OF EUMENINE WASPS II

BY KENNETH W. COOPER

E. N. Huyck Preserve, and University of Rochester, N. Y.*

None of the known associations that have evolved between mites and other animals seem more astonishing or noteworthy than that of the mite *Ensliniella trisetosa* Cooreman with the eumenid wasp *Ancistrocerus antilope* (Panzer). For these two, the very act of mating and intromission by the male wasp has come to provide a now essential thread of continuity between successive generations of *both* members of the alliance, as in turn does the act of oviposition by the female wasp. Extraordinary, too, is the fact that at one stage in the life history the male wasp treats the mite as a synoekete, whereas at this particular point the reaction of the female wasp is the very opposite, the mite now being abruptly dealt with as an intolerable synechthran. Bizarre as all this may appear to be, and as puzzling as the evolutionary steps are that gave rise to the involved interlacing of the lives of these two animals, it is possibly no more than a striking variant of a wide-spread, yet little-known, pattern of association of mites with eumenid wasps. Significantly, eumenid wasps regularly associated with mites occur on each continent, and such alliances are not restricted to a particular geographic area.

As a glance at any large and extensive collection of vespid wasps will show, adults of one or more species of *Allodynerus, Ancistrocerus, Monobia, Montezumia, Nortonia,* and *Parancistrocerus,*

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among others, habitually harbor characteristic deutonymphs. The life histories of these wasps and their mites, no less the mutually adaptive modifications, offer most promising subjects for evolutionary enquiry. Furthermore, it may be expected that the ultimate unravelling of the presumably linked and correlated phylogenies of the wasps and their mites will go far to assist in drawing some realistic and useful generic limits, of world-wide validity, within the vast and perplexing odynerine complex that comprises most of the Eumeninae.

The aim of this account, then, is to provide an initial description and analysis of some of the relations that exist between a larval mite and an adult eumenine wasp, in this case between the acarine *Ensliniella trisetosa* and the eumenine wasp *Ancistrocerus antilope*. The male and female wasps of this study have emerged from their nests and are foraging and mating, and the females are provisioning and masoning new nests for the next generation. The mites are all at the deutonymph stage, clinging continuously and tenaciously to the wasps, their vehicles, except at moments of crisis in their larval life brought about by the reproductive behavior, and reproductive functions, of their hymenopterous hosts. The nest, the prey, and some of the activities of the wasp, *Ancistrocerus antilope,* have been discussed in an earlier report (Cooper 1953). The relations of the adult mite to the immature wasp will be the subject of the third paper in this series.

The Wasp and the Deutonymph

Nearly any collection of insects having specimens of the large, yellow-marked, predominantly black, holarctic eumenid wasp, *Ancistrocerus antilope,* will contain within the series a number of males whose posterior and lateral propodeal faces bear varying numbers of deutonymphs of the saproglyphid mite *Ensliniella trisetosa* (Plate 1, figs. 1–3). When the total load of mites is a large one, say 280 or more, the lateral and posterior faces of the propodeum are colored a tawny brown by the closely packed mites, and such wasps are easily distinguished in the field. Curiously enough, while males bearing mites are ordinarily common enough in collections, few female wasps are to be found that carry such mites on the propodeal faces, or elsewhere on the body surface.

The few female wasps that do carry propodeal mites rarely have more than 14–19 deutonymphs clinging to them, and usually not more than 4 to 6. The distinction between the sexes in this regard reflects field experience reasonably well: *most* male wasps bear large propodeal loads of deutonymphs, at least early in their imaginal life, whereas *few* female wasps carry deutonymphs on their propodea, and those that do possess only small numbers of mites in these areas.

The deutonymph of *Ensliniella trisetosa* (text-fig. 1; *cf.* fig. 1 in Cooreman 1942) [1] is flattened and more or less broadly elliptical, being about 1.5 × as long (310 μ) as wide (206 μ). Not only does it differ markedly in shape from the other described ensliniellline deutonymphs that occur on eumenine wasps, namely Vitzthum's (1925) *Ensliniella parasitica* [recorded from *Allodynerus* (*Lionotus*) *delphinalis* (Giraud) and *A.* (*L.*) *floricola* (Sauss.)] and Zachvatkin's (1941) *E. kostylevi* [known from *A.* (*L.*) *rossi* (Lepeletier)] but, as Cooreman points out, the three long hairs and single ventral apophysis terminating the tarsus of the last pair of legs, as well as the approximation of the posterior edge of epimerite-II to the anterior margin of epimerite-III, allow easy recognition of *E. trisetosa.* In *E. parasitica* Vitzthum, which occurs in Europe and Russia, the idiosoma is smaller and more slender, being approximately twice as long (250 μ) as wide (124 μ); the tarsi of the fourth pair of legs each have two long terminal hairs, and two apophyses; finally, the second epimerite is remote from the third (*i.e.,* it is "free").[2]

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[1] Cooreman (*op. cit.*) described *E. trisetosa* from deutonymphs occurring on *Ancistrocerus antilope* collected at Bellaire and Beyne-Heuzay, Belgium, and has apparently also observed deutonymphs of this species on *A. parietinus* (Linn.) as well. Material that I have sent him from my studies, including eggs, tripodous larvae, protonymphs, deutonymphs, and adults of the mite, has led Cooreman to the conclusion that a new genus must ultimately be drawn for *E. trisetosa.* At this point it may be remarked that the differences in shape between my figure of the deutonymph, and Cooreman's, are very likely reflections of different methods of killing and preservation. Zachvatkin's (1941) figures of the deutonymph of *E. parasitica* Vitzthum also differ in like fashion from Vitzthum's (1925) own figures.

Since the above was written, Cooreman (1954) has described *Kennethiella,* and the mite of this article henceforth should be known as *Kennethiella trisetosa* (Cooreman).

[2] The most easily accessible figure of *E. parasitica* is to be found in Baker and Wharton (1952), fig. 271, p. 343.

Fig. 1.—Deutonymph of *Ensliniella trisetosa* Cooreman in ventral view; fresh preparation.

Judging from Zachvatkin's (1941) account, there should be no great difficulty in recognizing the deutonymph of *E. kostylevi,* recorded from Russia. It is intermediate in shape, having a body length of about 1.7–1.8 × as long (250–280 μ) as broad (145–160 μ). It has but three lanceolate setae on the third tarsus, which

also lacks an apophysis or digitiform spine, whereas both *E. parasitica* and *E. trisetosa* have four lanceolate hairs on the third tarsus as well as a digitiform spine. Unlike both *E. parasitica* and *E. trisetosa,* in which the eyes are nearly contiguous on the apex of the notocephalon, *E. kostylevi* has the eyes separated by a distance equal to a full corneal diameter. Finally, as in *E. parasitica,* the posterior edge of epimerite-II is remote from the anterior margin of epimerite-III, and there are also two apophyses and two long hairs terminating the tarsus of the fourth pair of legs.

Acarinaria

The deutonymphs of *Ensliniella parasitica* and *E. kostylevi* have been found clustered within special abdominal chambers of their hosts that lie between the apparent first and second abdominal tergites. These chambers involve modifications of both of the abdominal segments, but especially of the anterior articular face of the apparent second tergite. Here the variably depressed, transverse basal furrow is roofed over by a reflexed exoskeletal lamella, often of special form, derived from the anterior margin of the apparent second tergite. Such modifications are also characteristic of our very diversified North American mite-bearing eumenines of the genus *Parancistrocerus.*

In 1925 Bequaert extended the definition of the term "*acarinarium*", introduced by Roepke (1920) for the enclosed acarid chambers of xylocopid bees, to include variously placed and constructed integumental cavities that serve as abodes for mites in certain adult eumenine wasps. Since then, the term has come into general usage in this way by taxonomists. As mentioned above, males of *Ancistrocerus antilope* regularly carry loads of *Ensliniella trisetosa* in characteristic sites on the propodeum. Even though these deutonymph ladened loci are hardly chambers, I shall term them acarinaria, and thus use "acarinarium" in a more general way than hitherto, applying it to any surface or anatomical feature of an insect, enclosed or not, external or internal, that regularly serves as an abode for mites.

The Propodeal Acarinaria of the Male Wasp

The thorax of *Ancistrocerus antilope* conforms closely with the usual anatomy in odynerine wasps, and the acarinarial sites upon it that regularly carry mites are propodeal. As commented below, there are few striking differences, if any, between the thoracic and propodeal anatomy of male and female *A. antilope*. The text diagrams (text-figs. 2–3, p. 156) illustrate the larger features of thoracic anatomy in eumenine wasps, and upon them the acarinarial areas of male *A. antilope* are shaded with diagonal lines.

The lateral propodeal acarinarium of each side, (text-fig. 2) corresponds for the most part with de Saussure's (1855) "face inférieure des flancs", or ventral lateral area of the propodeum (vap) as Bequaert (1918) terms this region. The lateral acarinarium is bounded dorsally by the lateral propodeal ridge (e–b). This boundary is not so abrupt and clean cut as the diagram suggests, but the gradual loss of the antero-posteriorly elongated, coarse sculpture of the dorsal lateral area of the propodeum (dap) forms a fairly well demarcated upper limit of the acarinarium. Posteriorly the conspicuous border of the inferior propodeal ridge (b–c) terminates the acarinarium. The acarinarium is separated from the metasternum below by the angulate ventral margin of the propodeum (d–c). Finally, the anterior face of the acarinarium is marked by the lower portion of the posterior margin of the mesepimeron (em).

For the most part, the surface of the lateral propodeal acarinarium is shining and very sparsely overlain with relatively short, decumbent, posteriorly directed, hairs. These hairs are somewhat more numerous and less decumbent along the inferior ridge, and are notably longer on the margins of the dorsal posterior angle (b) of the ventral area. Throughout the posterior two-thirds of the acarinarium, the hairs form stream-lines that converge on the large deep pit above the posterior end of the valvula (val).

Outside the acarinarial area there is an abrupt change in the character of the sculpture and pubescence. On the dorsal lateral area of the propodeum, and along the posterior face of the inferior ridge, the sculpture is coarse, and the pubescence long and erect. The sculpture of the declivous posterior face of the mesepimeron changes abruptly from a coarse puncturation to a fine

shagreen that contrasts markedly with the shining surface of the acarinarium. Here too, on the mesepimeron, the pubescence is long and erect.

The posterior acarinarium of the propodeum corresponds exactly with the so-called propodeal concavity (text-fig. 3, con). A sharp, lengthwise medial carina divides the acarinarium, each half of the concavity being irregularly pentagonal in shape. The more medial dorsal margin of the acarinarium is formed by the reflexed edges of the dorsal lateral areas (dap). The small triangular region below the post-scutellum (ps) in the diagram, and above the upper margins of the acarinarium, is a portion of the isthmus connecting the dorsal lateral areas of the two sides of the propodeum, partially hidden behind the salient dorsal angles (a). The remaining margins of the posterior propodeal acarinarium are successively: the superior propodeal ridge (a–b), the inferior propodeal ridge (b–c), and the posterior marginal rim of the propodeum (c–c) above the propodeal teeth (pt).

The surface of the posterior propodeal acarinarium is also shining and smooth in texture, even though there are large but shallow, more or less obsolescent punctures along its borders, except along the ventral margin above the propodeal teeth. The upper triangles of each half concavity (that is, the area of each half-concavity bounded by the dorsal end of the medial carina, the dorsal angle (a), and the dorsal posterior angle (b)) have such punctures over most of their surfaces, but these punctures are very shallow where they are remote from the edges. The remaining acarinarial areas, except at the margins, are smooth.

The hairs of the posterior propodeal face are quite long and more or less erect in the punctate areas. In the smooth regions the hairs slope downward, are semidecumbent and short, forming stream-lines toward the deep recesses in which each half-concavity terminates ventrally. When the posterior face of the propodeum is viewed directly, as in text-figure 3, the posterior marginal area of the propodeum (c–c) forms the posterior wall of these two recesses. The pubescence is sparse and shorter than elsewhere at the common junction of the ventral lateral propodeal ridge (d–c), the inferior propodeal ridge (b–c), and the posterior marginal rim (c–c); namely, approximately above point c in text-figure 3.

The propodeal acarinaria of the male wasp, then, are characterized in a general way by their shining integument and characteristically arranged pubescence. Furthermore each acarinarial area is provided with a deep basal recess, or pit, above the valvula, or below the posterior marginal rim, as the case may be. The least sculptured and least pubescent pathway from the posterior acarinarium to its adjacent lateral acarinarium of each side is located at the common junction of the propodeal ridges (c) as described above.

The Propodeum of the Female Wasp and of Related Species

The propodeal regions of female *Ancistrocerus antilope* are similar to those of the male wasp in their over-all morphology and limits, and there seem to be no truly striking disparities. The most marked differences lie in the more abundant and erect long hair occurring within the polished regions that form the acarinaria in the male, as well as the somewhat coarser sculpture everywhere. There is also a more pronounced brush of short, dense, erect hairs along the horizontal shelf formed by the ventral lateral propodeal ridge in its extent above the valvula. But these distinctions between the sexes are of degree only, and they are perhaps no more than simple reflections of the fact that the male propodeal acarinaria nearly always carry full loads of deutonymphs at some time in the life of the wasp, whereas normally those of most, possibly all, female wasps never carry large loads of mites. As will be shown, the female wasps only occasionally harbor mites on their propodea, and then usually in small numbers only.

Yet the fact that female *Ancistrocerus antilope* only occasionally harbor deutonymphs on their propodea, and then only in small numbers, need cast no doubt that these modified faces of the propodeum are acarinaria. Their normal freedom from mites is no consequence of a lack of suitability to the mite, or any want of attractiveness. Normal absence of deutonymphs from these sites in female wasps, as will be demonstrated, reflects a peculiarity of female behavior at one point in the life cycle. If a living female wasp, enclosed in a vial, is artificially infested with several hundred deutonymphs of *Ensliniella trisetosa,* the mites clamber quickly

over her body. Ultimately, often speedily despite the wasp's cleaning efforts, the deutonymphs come to rest in tight arrays and regular patterns in all the propodeal acarinaria, and ordinarily nowhere else, just as though they were riding a male wasp.

Finally, if the thorax of *Ancistrocerus antilope* is compared with that of *A. catskill* (Sauss.), for example, it will be seen that the two are very similar in their overall anatomy and proportions. But male and female *A. catskill* are only rarely infested with mites, and it is significant that their sculpture is coarser, their pubescence is more abundant and erect, and their defining ridges and recesses of the ventral lateral areas and concavity of the propodeum are relatively less developed than those of *A. antilope.* Furthermore, in the relatively infrequent cases of mite infestation of *A. catskill,* the deutonymphs may cling to the propodeum, but often they are located between the abdominal sternites and tergites (as sometimes happens in *A. tigris,* also). Lastly, deutonymphs that cling to the propodeum of *A. catskill,* or of *A. tigris,* generally do so in disorderly clusters. There seem no grounds for the recognition of acarinaria in these species.

Other *Ancistrocerus,* as for example *A. unifasciatus* (Sauss.) and *A. clarazianus* (Sauss.), differ markedly from *A. antilope* in their propodeal morphology, and are not known to harbor propodeal loads of mites.

The Size and Arrangement of Propodeal Loads of Deutonymphs

As just commented, male and female *Ancistrocerus antilope* differ sharply in their respective relations to the mite that is so widespread through the adult population of wasps. When male wasps are caught, they are generally found to be carrying deutonymphs on their propodea, whereas more often than not female wasps prove to have empty propodeal acarinaria. Thus in a sample of 277 of these wasps collected in the 12-week interval June 21–September 11 in 1951, and again in 1952, 128 (83%) of the 155 males carry deutonymphs on their propodea, but only 15 (12%) of the 122 females do so. The maximum load of deutonymphs carried by any male of this sample is 407, but the greatest propodeal load of any female is only 19. The mean load of the males carrying

mites in their propodeal acarinaria is 134 deutonymphs,[3] whereas the mean load of the ladened females is only 4.3. Although there is a marked sexual difference in propodeal mite loads, the disparity between the sexes reflects no corresponding difference in acarinarial areas available to the deutonymph. On the contrary, the average female *A. antilope* is larger than the male, and has an aggregate acarinarial surface fully as great as that of the male, and very likely greater.

Perhaps, at least rarely, female *Ancistrocerus antilope* do occur with moderate or even large propodeal loads of deutonymphs, although I have not yet encountered such. If they do, their loading patterns will be found to be similar to those of correspondingly ladened males, to judge from the final acarinarial disposition of deutonymphs in those few females on each of which I placed several hundred mites. Females that have small propodeal loads, as do the 19 females in the sample mentioned above, have the mites arrayed just as in similarly lightly infested males. Therefore the description which follows of the arrangement of deutonymphs in the propodeal acarinaria of male *A. antilope* will, in all likelihood, be found to fit correspondingly infested females equally well.

When wasps are killed and pinned in the usual way, they are generally wholly unsatisfactory for studies of deutonymph distribution among and within acarinaria, the data collected from them being subject to doubt and reservation. On the one hand mites are generally displaced at pinning, if not during the struggles of the wasps in the killing bottle. On the other, deutonymphs seem considerably more resistant on the whole to cyanide and other fumes. They may later recover, break ranks on the moribund or pinned wasp, and become scattered in a wholly abnormal way, at times leaving or dropping off the specimen entirely.

The wasps that were used for a census of the mites were placed individually in shell vials (closed by netting) and kept alive until the mite loads could be removed and counted. Generally the mite loads were counted within 2–3 hours of capture of a wasp, and always on the day of capture. The wasps were very rapidly (4–5 seconds) etherized, and it is quite certain that there occurred no

[3] The number of males from which a count of the total mites was made is 100; males with propodeal mites totalled 90.

displacement from one acarinarium to another, nor was there any loss of mites from a wasp that I could discover. The mites were removed from the acarinaria with a fine, hooked " minute Nadel ", and counted under 95% alcohol.

The manner in which the mites arrange themselves in an acarinarium depends on a number of factors. Chief among these, it seems, are the structure of the acarinarium, the thigmotaxic responses of the mites, and the total number of mites involved. When one or a few deutonymphs are located in a lateral acarinarium of a male or female wasp, they center themselves at the deep pit above the posterior end of the valvula (text-fig. 2), with their dorsal surfaces outermost and their anterior ends directed toward the large, free acarinarial surface. A wasp bearing a moderate number of deutonymphs in a lateral acarinarium, say 15–40, usually has a fan-like array of mites extending out from this pit. The successive ranks of mites more or less underlap their adjacent neighbors that are closer to the pit, and overlap those away from the pit, much as shingles are laid on a roof. The mites, then, respond both to the structure of the acarinarium and to one another,[4] forming a rather tight-knit, coherent cluster. They do not locate themselves randomly or in scattered fashion within the acarinarium.

When a lateral acarinarium of a male wasp contains 75 or more deutonymphs, its surface may be completely covered with mites, yet not completely filled. With these larger loads, the mites that abut the outer margins of the acarinarium tend to be orientated so that the notocephalon is outermost, and the long axis of the mite more or less normal to the rim of the acarinarium. As more mites add themselves to a lateral acarinarium, the packing center shifts from the posterior pit above the valvula to a more nearly central location. With this shift, the more centrally located mites come to lie not like shingles on the surface of a roof, but at larger and larger angles to the propodeal surface, venter to neighbor's dorsum, and head end outward. This change to a new, closer packing order makes possible the addition of half again as many mites to the lateral propodeal acarinarium, and a load of 115 or more is

[4] Krumbiegel (1932) has suggested the terms *topothigmotaxis* and *homoiothigmotaxis*, respectively, to specify such responses.

not at all uncommon for each lateral acarinarium of heavily ladened males. When the load exceeds this number, the mites may slightly overflow the acarinarium along its anterior and dorsal margins, and even ventrally between the bases of coxae II and III. Such an overflow is not always the case, however, for the male that had the largest load of deutonymphs that I have counted within a lateral acarinarium, namely 139, had the mites densely packed, everywhere nearly perpendicular to the propodeal surface, and wholly within the morphological limits of the acarinarium. Very likely the deutonymphs are adfixed to the acarinarium, and to one another, by means of their suckers, and perhaps also by the palmate hairs of their tarsi. When removed from the acarinarium with a needle, they frequently maintain their packing to one another, forming coherent sheets that must be picked apart with needles for counting.

The posterior acarinarium of the propodeum has a lengthwise carina that divides it into two halves (text-fig. 3). When this acarinarium bears only a small number of deutonymphs, the mites behave as though two separate acarinaria are present. Thus all may be clustered in a small radiating fan from a single center of packing in one half-concavity, or they may be scattered among each of the four principal sites at which packing centers originate. These four sites are the angles at each end of the straight, recessed, basal edge of each half-concavity, immediately above the propodeal teeth (text-fig. 3, c–c). Each half-concavity ordinarily has its surface covered when it contains 30 or more mites. The mites then fan out from the basal recess, their head ends directed away from the base. With loads of this size and larger, the median carina that divides the concavity becomes hidden beneath the bodies of the mites, and the acarinarium now appears undivided. Although as few as 50 mites may cover the entire acarinarial surface of the two half-concavities, in the average wasp the posterior propodeal acarinarium can hold at least 80 deutonymphs when they are arranged in tight packing order. At this point, or even with smaller numbers of mites, the deutonymphs may spill over the dorsal margin of the posterior acarinarium, extending onto the most dorsal, medial portion of the propodeum, and still further onto the posterior face of the post-scutellum. The largest load of

deutonymphs lodged in the posterior propodeal acarinarium of a male wasp of the censused sample was 130, and these were spread dorsally onto the post-scutellum. The male wasp that carried 407 deutonymphs in its propodeal acarinaria had this maximum observed load. The left propodeal acarinarium lodged 139 deutonymphs, the right acarinarium 138, and the posterior acarinarium 130. Very likely this wasp approached, or had even reached, the greatest load of *Ensliniella trisetosa* deutonymphs that its propodeal acarinaria could hold.

Since the male just noted was carrying a near maximal load, it is not surprising that the right and left sides had very nearly equal numbers of deutonymphs. What is surprising is the fact that ordinarily male wasps that have from 150–350 propodeal deutonymphs, carry very nearly equal loads of deutonymphs in the two lateral acarinaria. As the total propodeal load of deutonymphs decreases, the relative loss tends to be greatest from the acarinarium of the concavity. In general, the loading relationship may be written:

[concavity] $<$ [left acarinarium] = [right acarinarium].

When a heavily ladened male wasp has the mites stripped with a needle from one lateral acarinarium, and with its reduced load is then isolated in a vial, it is not unusual for the mites to redistribute themselves (within the span of a day or so) so that very nearly equal loads are again carried in the two lateral acarinaria. These new lateral acarinarial loads of course are usually smaller than the original lateral loads. But their sum is greater than the original load of the unstripped lateral acarinarium, and the gain is at the expense of the deutonymphs carried in the acarinarium of the concavity. It is likely, then, that marked asymmetry of lateral acarinarial loading in a male carrying 150–350 propodeal deutonymphs indicates a recent reduction (or loss) of mite load from the propodeal acarinaria. This balancing of the wasp's ballast of mites brings to mind similar tendencies on the part of the mite *Antennophorus* on the ant *Lasius*. Here, however, the mites are relatively large when compared with their host, and their numbers are small (*ca.* 1–7 per ant) (*v.* Wheeler 1910).

Finally, it should be remarked that a few wasps are taken each season that have one or a small number of deutonymphs riding

upon them in some extra-acarinarial position. Such deutonymphs may occur on the head, the thorax proper (especially in the fossae to each side of the scutellum), or on the abdomen of the wasp in sites where hairs are few, short, or decumbent. They do not seem to cling to the legs or mouthparts, but this cannot be owing to the activity of these members alone. Curiously enough, the commonest site for such stray mites is on the forewing, principally along the cubital vein or in the first submarginal cell. The greatest number of mites occurring outside an acarinarial area for any wasp of the sample was 12. These occurred on the left (9) and right (3) wings of a male wasp that bore a total of 341 mites. The remaining 329 mites were located in the left (122), posterior (95), and right (112) propodeal acarinaria.

The Genital Acarinarium of the Male Wasp

Of course it is common knowledge among hymenopterists that male *Ancistrocerus antilope* carry external loads of deutonymphs, although no earlier study seems to have been made of the loads and their packing, or of the acarinaria. It is much less well known that internally male wasps may also carry very considerable numbers of the same deutonymph, *Ensliniella trisetosa,* in addition to those lodged in the propodeal sites. Bequaert (1944) was the first to call attention to the fact that the mites ". . . sometimes invade the interior of the seventh abdominal segment of the male." It will later be shown that this " invasion " has a remarkable history and a notable consequence.

Although, from time to time, males of *Ancistrocerus antilope* are found that do not carry mites on any of the propodeal acarinaria, dissection of such males discloses masses of deutonymphs within the genital chamber more often than not. In the sample of 155 males, 18 (12%) have mites in the genital chamber only, and 71 (46%) have mites both on the propodeum and within the genital chamber. Despite the fact that the genital load of deutonymphs may be a large one (180 or more), there is no specially striking departure in gross morphology of the male genital chamber of *A. antilope* from that of other species of *Ancistrocerus.* Yet it is relatively hypertrophied and notably broad—with little doubt modifications that are related to its now normal but supplemental function as an abode for deutonymphs.

Deutonymphs that are carried internally by a male wasp are generally restricted to a broad, shallow space lying between the combined internal surfaces of the eighth plus ninth sternites and the ventral surface of the phallus plus its extrinsic musculature (text-fig. 4, p. 156).[5] This ventral, slightly concave, internal acarinarial space is roughly pentagonal. The apex of the ninth segment is nearly truncate, being only shallowly emarginate, while the confluent lateral margins of sternites nine and eight of each side are moderately divergent. Protractor muscles of the ninth sternite, originating at the apex of the median apodeme (or spiculum) of the ninth sternite, and inserting on the posterior lateral margins of the eighth sternite, mark off the anterior lateral margins of the genital acarinarium and complete the pentagon (text-fig. 4). The phallus, and the ventral musculature that is attached to its gonobase, lie immediately above the acarinarium. The actual roof and floor of the acarinarium is the transparent, colorless fold of body wall that lines the ventral genital chamber. As the integument of sternite eight is a transparent amber or light brown, and that of sternite nine is a transparent brown that progressively darkens over the apical half or two-thirds of the sternite, the deutonymphs may easily be seen from below through the ventral wall of the acarinarium so long as the ninth sternite is not strongly retracted into the abdomen.

The Size and Arrangement of Internal Loads of Deutonymphs in the Male Wasp

Unlike the deutonymphs in a thoracic acarinarium, the mites of the ventral genital chamber of the male are not free to leave, but are imprisoned. They can exit from the enclosure only if the tip of the wasp's abdomen is opened. Pinned males of collections frequently retain their full genital complement of mites for this

[5] Note that the true ninth sternite is the "seventh sternite" of the taxonomist. The systematists ordinarily assign the propodeum (= abdominal segment 1) to the thorax, commencing count with the apparent first (= 2nd) abdominal segment. The eighth sternite is also overlooked because it is not normally visible without dissection, being telescoped within the apparently penultimate segment. The works of Duncan (1939), Snodgrass (1941), and especially Michener (1944), will prove helpful to the reader, for they provide more detailed descriptions of the genital anatomy of aculeates than can be given here.

reason, even though the mites of the propodeum may have scattered and, in part at least, have left the host. For study of the packing and arrangement of deutonymphs in a genital chamber, it is nevertheless necessary to etherize wasps quickly, and to open the chamber for inspection by prying apart the appressed apices of the eighth tergite and ninth sternite. The phallus is then grasped with forceps, pulled from the chamber, and reflected dorsally. The full extent of the ventral chamber is open to view with a binocular dissecting microscope when this is done. Rapid etherization is necessary, as well as immediate inspection thereafter, because the mites in a dead wasp break ranks. Even though a male wasp whose abdominal tip has not been parted in death may retain all the deutonymphs of the genital acarinarium following cyanide fumes, the mites themselves will frequently be found to have survived the death of their host, to have broken their clusters, to have wandered within the interstices of the phallus, to the dorsal genital chamber, and so on, before dying.

In the sample of 155 male wasps, 89 (61%) carry mites in their ventral genital chambers. Eighteen of these wasps (12.3%) have mites nowhere else, and the remaining 71 (48.6%) have mites in both the ventral genital chamber and in the propodeal acarinaria. The maximum load carried in the ventral genital chamber of any of these males is 203 deutonymphs, and the mean load in the ventral genital chamber of the male is approximately 37 deutonymphs. The maximum *total* load in the genital chamber of any male so far observed by me is 238, but the subdivision of this load between the ventral and dorsal genital chambers was not determined (see p. 161).

When the numbers are average or large, the deutonymphs in the ventral genital chamber tend to form a thin, continuous sheet of mites, one individual in thickness, that covers the integument of the ventral floor of the ventral genital chamber. When the numbers of deutonymphs are large, 150 or more, the sheet of mites may be reflected dorsally onto the membrane immediately below the ventral base of the phallus. In such a case the sheet of mites forms an asymmetrical, cup-like configuration that is concave inwards. Regardless of whether there are many mites, or a small sheet of mites, whether the mites are on the ventral surface or on

the dorsal membrane at the anterior end of the ventral genital chamber, the mites of the genital acarinarium tend to face outwards toward the juncture of the eighth tergite and ninth sternite. This non-random orientation of the mites in their undisturbed array can be very striking.

Seventeen (11%) of the males also contained some deutonymphs *dorsal* to the phallus, principally just anterior to the anal papilla. The ventral genital chamber of most of these wasps was simply packed with mites, and in contrast the numbers of deutonymphs in the dorsal genital chamber ranged merely from 1 to 23, with a mean of only about 6 (actually 5.8) for these 17 male wasps. In the case of the male with 203 deutonymphs in the ventral genital chamber, as an example, only 3 mites were to be found in the dorsal genital chamber. It seems likely that the dorsal genital chamber of the male has only an ancillary role in harboring mites. It may be viewed with reserve as receiving the spill-over from very large loads of deutonymphs packed within the acarinarium of the ventral genital chamber. For this reason a number of mites in the dorsal genital chamber of a male having a small load of mites may be taken as partial evidence that formerly the wasp carried a significant load of deutonymphs in its ventral genital chamber.

Evidence for a Shift of Deutonymphs between External and Internal Acarinaria of the Male Wasp

The presence in male *Ancistrocerus antilope* of both external and internal acarinaria at once sets this species apart from all other known cases in which wasps regularly carry mites, and awakens a number of interesting questions about the bionomics of both mite and wasp. The first and simplest of these questions asks: In what ways, if any, are the internal and external loads of deutonymphs correlated? The answer is easily obtained: They are negatively correlated.

For most of the flight season, male *Ancistrocerus antilope* fall into four classes with respect to their loads of deutonymphs: (a) males having no mites at all; (b) males having mites in the propodeal acarinaria only; (c) males having mites in the genital

acarinarium only; and (d) males ladened with mites in both propodeal and genital acarinaria. Now there is a number of peculiar facts concerning these classes, and at first examination they may seem paradoxical.

On the one hand, the relatively few male wasps (about 6% of all males of the sample) that have no mites at all are either *newly emerged* (2), or more usually are *very old* (7) as judged from their stained and frayed wings, dull yellow coloration and lack of integumental bloom, lost tarsal joints, worn clypeus, and so on. On the other, it would be expected that wasps having mites in *both* the external and internal acarinaria would carry the largest loads of deutonymphs. Inasmuch as the propodeal acarinaria can accommodate upwards of 400 deutonymphs, and the genital acarinarium 200 or more, a male wasp maximally harboring mites in both these sites might carry as many as 600 deutonymphs, and perhaps more. Not only was the largest observed load merely two-thirds of this figure, but it was indeed carried by a wasp *without* mites in its genital acarinarium. There is no doubt that, by and large, male wasps with only propodeal mites carry the largest average total load. For the four classes of males the sequence with respect to size of mean load ($\overline{m}$) is:

a (0) c (51) d (119) b (244).

Although 155 male wasps were examined for the presence of externally and internally carried mites, exact counts of the actual numbers of mites harbored were made for a subsample of only 100 of these males. These counts are summarized in Table 1 in such

TABLE 1

The mean total loads of deutonymphs of *Ensliniella trisetosa* Coor. of mite-bearing male *Ancistrocerus antilope* (Panz.) whose genital chambers contain $\leqslant$ x % of the total load of deutonymphs. The first column states the inclusive range in percent of the total load (propodeal + genital) that is in the genital chamber; column 2 gives the number (N) of wasps in each category; column 3 lists the total number of mites carried by the N wasps; column 4 gives the mean total load ($\bar{m}$ load) of mites; and the last column gives the mean percent ($\bar{m}$ %) of the total load that is carried in the genital chamber. Six males devoid of mites are excluded from the table.

1 % Range of Total Load in Gen Ch	2 N	3 Total Mites	4 $\bar{m}$ Load	5 $\bar{m}$% in Gen Ch
0	39	9,529	244	0
> 0– 25	6	1,129	188	4
26– 50	8	996	125	32
51– 75	12	1,485	124	64
76– 95	23	2,355	102	87
96–100	6	306	51	99
Totals	94	15,800	168 (114) *	24%

* The bracketted mean of 114 is the mean total load of deutonymphs carried by the 55 male wasps that have mites in their ventral genital chambers.

a way that the relationship is expressed between the total load of mites and the percentage of that total load that is carried in the genital acarinarium. Ninety-four percent of the male wasps of the Rensselaerville, N. Y., collections carry mites, and four significant conclusions may be drawn from the distribution of deutonymphs among the acarinaria of these wasps.

First, the largest mean total load of deutonymphs (= 244) is carried by that class of males (comprising 41% of the mite-carrying males) in which the wasps have no deutonymphs located in the genital acarinarium.

Second, wasps with the largest mean percentage (= 99%) of their total load of deutonymphs located in the genital acarinarium have, in turn, the smallest mean total load of deutonymphs (= 51).

Third, the mean total load of deutonymphs (= 114) carried by wasps having some or all of their mites located in the genital acarinarium is roughly half that of the wasps bearing all their deutonymphs propodeally.

Fourth, with *increasing* mean percentages (of the total mite loads) of deutonymphs that are located in the genital acarinarium, there is a progressive *decrease* in the mean total load of deutonymphs carried. In other words, there appears to be an ordered increase or decrease of the total mite load that accompanies a shift in the distribution of the population of deutonymphs between the genital and propodeal acarinaria.

Of a number of explanations that could formally account for these facts, the two that are simplest seem to be these. With the passage of time, either (1) male wasps accumulate larger and larger loads of deutonymphs, or (2) they initially have a large load that is not thereafter exceeded, but which is dissipated with time. In either case, the changes in the size of the population of mites being transported bears a regular and striking relationship to the acarinarial sites that are loaded: large loads are chiefly propodeal only, intermediate loads are borne by simultaneous loading of both the genital and the propodeal acarinaria, and the smallest loads are principally carried by the genital acarinarium only. We now ask: Do male wasps gain or lose mites as they grow older, and is the shift from the genital chamber to the propodeum, or the reverse?

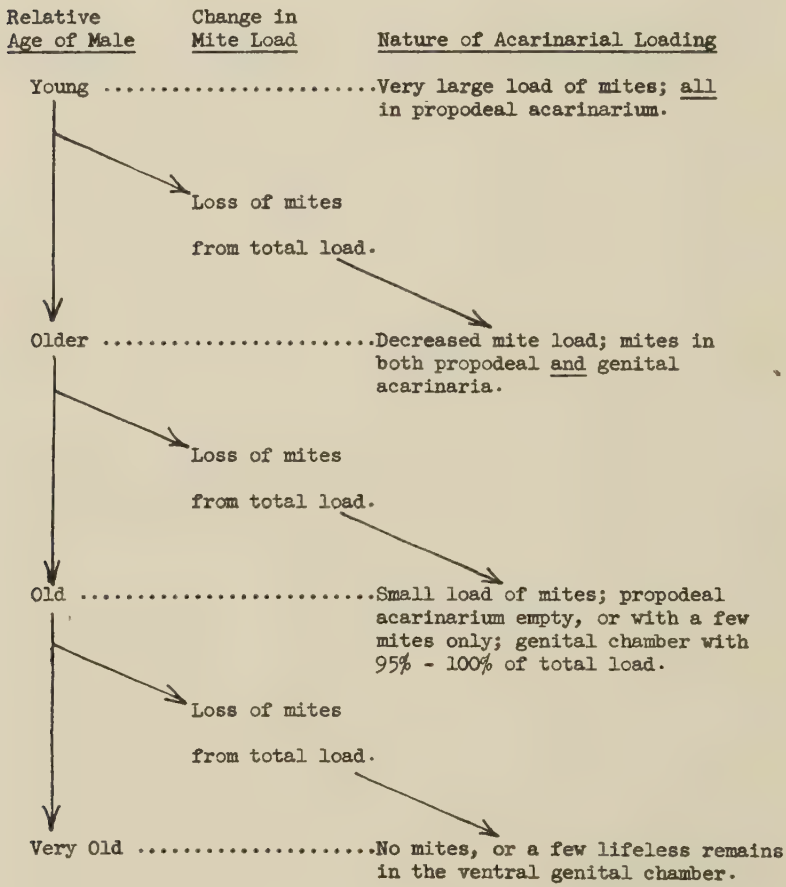
There can be no doubt that the male wasps lose mites as time passes, for as a class male wasps bearing only propodeal loads are the more recently emerged (that is, they are the youngest imagos), and that those with genital loads are the older. Thus lively males with glistening, unfrayed wings, bright yellow livery, soft integumental bloom, and an overall appearance that suggests that they have yet to meet the trials of their adult existence, are nearly always bearers of large loads of deutonymphs, and these deutonymphs are restricted to the propodeal acarinaria. As would be expected from this, the first males to be captured in the early season, and those of the second brood that emerges early in August,

are almost always characterized by heavily ladened propodea and empty genital chambers. Conversely, frayed and battered males carry genital loads of deutonymphs, or none at all. Late August's and most of September's male *Ancistrocerus antilope* are nearly all bearers of genital loads of deutonymphs, or without mites, and I have never encountered a male with the stigmata of age that carried a large load of deutonymphs exclusively situated in the propodeal acarinaria. The shift of mites, then, is from the propodeum to the genital chamber, and the initial load must be exclusively propodeal.

It must now be emphasized that the shift of mites from propodeal to genital acarinaria that regularly occurs in the life of nearly all male *Ancistrocerus antilope* is accompanied by sizeable losses of deutonymphs from the initial and subsequent loads. When the first shift occurs from the propodeum to the genital acarinarium, it may be inferred that the propodeal load (and hence the total load) is decreased by approximately one-half. About half of the deutonymphs that are lost from the propodeal acarinaria are to be found in the ventral genital chamber of the male. The other half are truly lost from the wasp, for they are no longer to be found on or in the male wasp. If no more than this were known, it would be possible to view the loss of perhaps a quarter of the total initial load of deutonymphs as a consequence of some special event accompanying the translation of the mites from the propodeal acarinaria to the genital chamber. This is certainly not the case, however, for wasps with both propodeal and genital loads, or with genital loads only, also suffer a stepwise decrease in their total loads of deutonymphs with the passage of time. These losses are also of sizable packets of mites, namely from 30–100 deutonymphs at a time. It makes little difference how the total load is borne, loss from it is not gradual, but is abrupt and by masses of mites rather than by an individual or two. It is this "quantal" loss of mites that accounts for the initially puzzling fact that the sum of the genital and propodeal loads of male wasps carrying mites in both acarinarial sites is less than the sum of the mites carried by males having propodeal deutonymphs only. The history of the loads of deutonymphs of *Ensliniella trisetosa* borne by adult male *Ancistrocerus antilope* is summarized in diagram 1.

DIAGRAM 1

Resumé of the history of deutonymphal loads of *Ensliniella trisetosa* carried by adult male *Ancistrocerus antilope* (see text).



Experiments on the Shift of Deutonymphs between Acarinaria in the Male Wasp

There are two obvious ways in which the shift of deutonymphs between acarinaria might occur. The mites could be shifted by

the wasp itself, or perhaps the deutonymphs themselves break ranks and migrate from the propodeum to the genital chamber. In either case it might also be that the demonstrated loss of deutonymphs from the total load occurs primarily at other times than that of a shift between acarinaria. For statistical reasons that will not be gone into, it seemed very likely that the shift and loss are but two aspects of one event. A number of simple experiments, now to be summarized, were undertaken to discover answers to the questions: what induces the shift of deutonymphs from external to internal acarinaria, how are deutonymphs lost from the total load, and what is their fate?

(1) *The effect of time alone.*—Eight male wasps with heavily ladened propodea, and empty genital chambers, were individually maintained, in seemingly good health, in gauze-covered jars for periods of two to nearly three weeks. In none was there an acarinarial shift, nor a discoverable loss of deutonymphs. Wasps with genital loads, similarly maintained for a week, suffered no detected loss of mites from their genital chambers. Evidently time alone is not a sufficient cause for either shift or striking loss of deutonymphs.

(2) *The effect of mechanical disturbance.*—The possibility was tested that the propodeally situated deutonymphs seek internal shelter, where presumably they would be free from external molestation, once their propodeal packing order is disturbed. This seemed an attractive possibility, for it might also account for some loss of mites.

It is difficult to arouse the mites individually, but 18–20 male wasps each had their propodeal loads brushed, disrupted with a dissecting needle, or actually stripped and placed on the walls of the shell vial holding the wasp. In all cases the mites reassembled on the propodeal acarinaria, establishing nearly equal masses in the right and left lateral propodeal acarinaria, and refilling the acarinarium of the posterior face. Except for the relatively small number of mites that crept into the gauze stopper, or became stuck to the vial, there was no great loss of deutonymphs from any wasp, nor was there entry into the genital chamber in any case. Simple mechanical disturbance is evidently not a sufficient cause for shift. Had the wasps from which the mites were actually stripped not

been kept imprisoned within their vials, these mites would have been lost with the escape of the wasps.

(3) *The effect of the presence of other wasps.*—(a) A group of a half-dozen males were placed together in a pint jar for nearly a week. During this time there were struggles and conflicts between some of the wasps. Regrettably I was unable to discover whether there had been any shift of deutonymphs between the males, but there was definitely no entry of deutonymphs into the genital chamber in any case, nor any notable loss of mites from the wasps.

(b) A second series, in which several males without mites were included, proved that males without propodeal mites can (and did) acquire at least small numbers of propodeal mites (maximum = 23) from their heavily ladened associates. Again there was no case of entry to a genital chamber.

Simple conflict and association with other wasps is evidently not a sufficient stimulus for a deutonymphal shift from propodeum to genital chamber. However, such conflicts and association may result in some loss of deutonymphs to unladened wasps.

(4) *The effect of overloading.*—Only two males were subjected to potentially massive overloading by being enclosed in vials to which a thousand or more deutonymphs, in addition to those already loading the propodeum, had been added. Very interestingly, these males scraped antennae and legs, thorax and abdomen, in a frantic manner and in a very evident effort contrived to free themselves of excessive mites once their propodea were clearly overloaded. They behaved exactly as *Ancistrocerus tigris* does when placed with deutonymphs of *Ensliniella trisetosa,* with which it is not normally associated. In any event, no deutonymphs entered the genital chambers of the two male *A. antilope* as a response to overloading. This result, of course, was to be anticipated in view of the fact that the most heavily ladened males carry only propodeal loads under natural conditions.

(5) *The effect of opening the genital chamber.*—As pointed out earlier, the genital chamber is so tightly closed in the living male wasp that without doubt it must be opened by the male wasp if deutonymphs are to enter it. Since, in the above experiments, it could not be known that the genital chamber had been opened (although assuredly the males of experiments 1 and 3 had defecated

repeatedly), it is possible to maintain that a shift to the genital chamber did not occur *because* opening of the genital chamber is really the essential stimulus for the deutonymphs to undertake a shift.

A half dozen male wasps had their ninth sternites trimmed or notched with iridectomy scissors in such ways that the genital acarinarium remained permanently open to the outside. Such males lived but a few days at best (perhaps dying because of uncontrolled and excessive water loss by evaporation), and in no case did the deutonymphs leave the propodeal acarinaria and enter the genital acarinarium.

Even if the genital chamber of the living wasp is opened by the male itself, the deutonymphs do not seem to break ranks, leave the propodea, and enter the genital chamber. A male wasp, held in the fingers by its legs, will repeatedly stab the fingers with the phallic spines (parameral spines), and at such a time—if mere opening of the genital chamber were a sufficient stimulus—the deutonymphs would be expected to show some evidence of response. They do not, unless mechanically displaced by the fingers or the struggles of the wasp, and so once again mere opening of the genital chamber seems not to be an adequate stimulus to induce a shift.

On the other hand, if the mites are stripped from a male wasp which has a permanently opened genital chamber, some deutonymphs do enter the chamber as they clamber back over the wasp. A sizeable load could undoubtedly be built up in such a wasp by repeatedly scraping off the deutonymphs that settle in the propodeal acarinaria, and permitting them to climb again and again on the wasp. This experiment, if it suggests anything about natural events, shows that it is not sufficient for the genital chamber to be open, but that it is also necessary for the mites to be freely creeping about the abdomen of the wasp if the genital chamber is to be loaded.

(6) *The effect of visits to flowers.*—Wasps kept in the laboratory had been fed sugar water, maple syrup, honey, saliva, and insect blood. It seemed possible that when a wasp visits flowers, it may acquire or lose mites, and that furthermore shifts of deutonymphs to internal acarinaria might be consequences of some

special activity of the male in a flower head. Male wasps were accordingly kept a week or more, and fed each day exclusively with fresh flowers of *Pastinaca sativa, Spiraea latifolia,* and *Solidago canadensis.* As far as I could determine, these males did not lose any mites to the flowers; certainly there was no shift of deutonymphs from propodeal to genital acarinaria.

Other small-scale, individual experiments were made, but none gave a result suggesting that they would be worthy of repeating on a larger scale. Indeed, toward the close of the first season of study, the cause and mechanism of the shift of deutonymphs seemed an insoluble puzzle, at least insoluble along the lines of enquiry I had been following. It is true that a loss of mites, at least in part, could be accounted for in a formal, if not satisfying manner. For example, it is shown above that deutonymphs can shift to other wasps *if* the other wasps are closely confined with infested males. Or deutonymphs can be lost from the genital chamber of a male wasp bearing a large genital load of mites when the wasp stabs its captor with its parameral spines in simulated stinging. Anyone holding a male *Ancistrocerus antilope* bearing a large genital load of mites can easily verify this by noting the dozen or more deutonymphs to be found creeping on the fingers after release of the wasp.

At this point then, what it may be that brings about the shift of the deutonymphs from the propodeum to the genital chamber of the male wasp remained a major puzzle. Since young male wasps regularly possess propodeal loads of deutonymphs, whereas female wasps of all ages usually do not, it had been thought that a difference in the autecology of male and female wasp might prove sufficient to explain their difference in phoresy of mites. A somewhat analogous case, for example, might be that of the deutonymphs of *Caloglyphus julidicolous* which Lawrence (1940) has found to aestivate within the enclosed genital apparatus of male millipedes (*Doratogonus flavifilis* Peters, and *Ardiophyllum* sp.) in Eastern Transvaal, Africa. But it now seems wholly out of the question that the deutonymphs of *Ensliniella trisetosa* seek no more than protection from some environmental factor in the genital chamber of male *Ancistrocerus antilope.* A simple ecological interpretation of the problem seems unlikely, although such an ex-

planation may be found that will make understandable the evolutionary origins of the alliance of this mite and wasp.

The vectorial change in the size of the mite loads, and their vectorial translation with time from the propodeum to the genital chamber of the male suggested, when coupled with the essentially negative results of the experiments described above, that the relationship of the female wasp to the male might prove a fruitful line of investigation. For example, it seemed that the propodeal mite load of the male may be deranged during courtship or mating, perhaps even partially scooped into the genital chamber of the male as the phallus scrapes past the postero-lateral faces of the propodeum, as may be the case prior to intromission. If so, the female could provide the key to both genital loading and losses of packets of mites by the male wasp. Remarkably, she does, although genital loading is brought about in another way.

The Relationship of the Female Wasp to the Deutonymph

It was not possible to test immediately and directly the suggested role of the female wasp as an indispensible agent or ally in the translocation of deutonymphs on the male wasp, for a prolonged cold and rainy spell made collection of suitable specimens out of the question. Nevertheless discovery of packets of deutonymphs in the dissected genital chamber of relaxed pinned specimens, and thereafter study of the actual numerical distribution of the deutonymphs within the female genital chamber, and of the presence or absence of genitally-borne deutonymphs in young and old imaginal females, collectively granted sufficient insight to the problem to make possible a detailed prediction of a number of the cardinal features of the alliance of the mite and the wasp. The evidence of these dissections alone makes it highly probable that the life cycles of the two organisms have become inextricably interlaced through an exacting evolutionary coadaptation.

There are six principal points, and the evidence from which they are drawn is summarized in Tables 2 and 3.

TABLE 2

The distribution of deutonymphs of *Ensliniella trisetosa* Coor. in acarinaria of adult wasps of the total sample of 155 males and 122 females of *Ancistrocerus antilope* (Panz.) from Rensselaerville, N. Y. Column 1 describes the overall loading of the wasps with deutonymphs, 2 and 2′ give the number (n) of male and female wasps so ladened, 3 and 3′ state the corresponding percent (% of total) for the *total* sample of males or females, and 4 and 4′ give the corresponding percentage (% of those with mites) for each sex of only those wasps of the sample that carry mites.

	155 Male Wasps			122 Female Wasps		
1	2	3	4	2′	3′	4′
Acarinaria Harboring Mites	n	% of Total	% those with Mites	n	% of Total	% those with Mites
Propodeal and/or Genital	146	94.2	100.0	115	94.3	100.0
Propodeal only	57	36.8	39.0	1	0.8	0.9
Genital only	18	11.6	12.3	95	77.9	82.6
Propodeal and Genital ..	71	45.8	48.6	19	15.6	16.5
Propodeal*	128	82.6	87.7	20	16.4	17.4
Genital*	89	57.4	60.9	114	95.8	99.1

* These two lines give the corresponding information for the *total* frequencies of propodeal and genital acarinarial loading regardless of whether or not other acarinaria also harbor mites.

First, male and female wasps are actually equally frequently infested with mites, 94% of each sex harboring deutonymphs in one or more of their acarinaria. In effect this means that the deutonymph of *Ensliniella trisetosa,* contrary to general belief, normally and regularly infests *Ancistrocerus antilope* without distinction as to sex of the wasp, although the actual distribution of the deutonymphs among external and internal acarinaria is different in the two sexes.

Second, young (or newly emerged) female wasps bear no deutonymphs at all, whereas older females normally carry deutonymphs in their genital chambers. In the genital chamber of very old females, however, there may be no mites at all, or in some cases only the remains of a few deutonymphs. It may be inferred from this that female wasps acquire their loads of deutonymphs *after* emergence from the nest, and then dissipate them with time.

Third, no female wasp has been encountered bearing large numbers of deutonymphs in the propodeal acarinaria only. In fact, if a female wasp has propodeally situated mites, then she almost invariably carries mites in her genital chamber also (see Table 3). Furthermore the mean load ($\bar{m} = 70$) of female wasps carrying propodeal mites is greater than that ($\bar{m} = 47$) of females without propodeal mites. Consequently those females bearing propodeal mites are, on the average, very probably less removed in time from the event by which deutonymphal loads are acquired.

TABLE 3

Comparison of maximal (max), mean ($\bar{m}$) and percentage (%) deutonymphal loading of all acarinaria of male and female *Ancistrocerus antilope* (Panz.) by *Ensliniella trisetosa* (Coor). The maxima and means are those for subsamples of 100 male and 50 female wasps from Rensselaerville, N. Y. The "percentage loadings" (% of total mites) are the percentages of the total deutonymphs found on the 100 male (15,800 deutonymphs) and 50 female wasps (2,267 deutonymphs). 94% ± 2.4% of the males and 88% ± 4.6% of the females in these subsamples carried deutonymphs; indeed 94% of each sex of the total sample carried mites (see Table 3).[6]

Loading of Deutonymphs	Male Wasps			Female Wasps		
	Max	$\bar{m}$	% of Total Mites	Max	$\bar{m}$	% of Total Mites
Total	407	158	100.0	135	45.3	100.0
on Propodeal Faces	407	121	76.4 ± 0.3	14	0.76	1.7 ± 0.3
posterior face	130	30	19.0 ± 0.3	10	0.06	0.1 ± 0.07
right face	138	46	28.4 ± 0.4	14	0.4	0.9 ± 0.2
left face	139	45	28.9 ± 0.4	10	0.3	0.7 ± 0.2
in Genital Chamber	206	37.4	23.6 ± 0.3	132	44.6	98.3 ± 0.3
dorsal chamber	23	0.7	0.4 ± 0.04	131	40.5	89.3 ± 0.7
ventral chamber	203	36.7	23.2 ± 0.3	18	4.1	9.0 ± 0.6

[6] There is no essential difference between the sexes in these subsamples (or between them and the total sample) in percentage infestation with deutonymphs. The difference between them is only 1.15 × the standard error of the difference. A deviation as great as or greater than this may be expected with a P of 25%.

Fourth, the maximum and mean deutonymphal loads of the female wasp (max = 135; $\overline{m}$ = 45) are both much smaller than the corresponding statistics for the male (max = 407; $\overline{m}$ = 158) (Table 3). Indeed they correspond very favorably with estimates of the magnitude of the individual losses of deutonymphs that occur sporadically in the adult life of the average male wasp.

Fifth, the major acarinarial site of the female wasp is the *dorsal* genital chamber, whereas that of the male genital chamber is *ventral* (Tables 2, 3). Thus the mean deutonymphal load of the ventral genital chamber of the male wasp is 37, and that of the dorsal genital chamber only 1, whereas for the female wasp the corresponding statistics are 4 (ventrally) and 40 (dorsally). Since in Lamb's (1922) terminology, there is a modified *inverse correlation* of the genital regions of male and female wasp at mating, the ventral genital chamber of the male becomes more or less confluent with the dorsal genital chamber of the female during intromission. Consequently, were deutonymphs to pass to the female from the ventral genital chamber of the male, they would be expected to be found in the dorsal genital chamber of the female, as indeed they are.

Sixth, and lastly, at least some of the deutonymphs in the dorsal genital chamber of the older females appear physically different from deutonymphs of the propodeal acarinarium of male or female wasp, and from those of the genital acarinarium of the male. These deutonymphs are more pallid and milky in coloration, and appear very slightly bloated, suggesting approach to ecdysis and passage from the deutonymphal stage.

Inference from these facts, and from those set forth and analysed above for the male wasp, lead directly to the following, now quite obvious, conclusions. *Ensliniella trisetosa* assuredly lives with *Ancistrocerus antilope* throughout the whole life cycle of each member of the alliance, and the adult forms of the mite are to be found in the nest of the wasp, perhaps as paraphages. Male wasps must emerge from the nest bearing propodeal loads of deutonymphs. On the other hand, female wasps must emerge from the nest devoid of deutonymphs, even though possessing nearly identically developed acarinaria, and then acquire deutonymphs from the males at mating. Thus the loss of deutonymphs from adult male wasps

must in large part take place by transfer to female wasps. In turn, losses of deutonymphs from female wasps must be chiefly (? or only partly) by deposition in the cells of the new nest during its construction or provisioning. Since adult male wasps must emerge from their cells with full deutonymphal loads, and females must emerge without deutonymphs, it would seem that whatever factors determine that a particular egg will be fertilized, hence diploid and giving rise to a daughter, must also decide that normally deutonymphs will not be released to the cell containing a diploid egg.

All these inferences have been put to test. As will be shown following description of the female genital chamber and its acarinarium, the act of mating does in fact result in both the translocation of deutonymphs on the young adult male wasp, and in a loss of mites from the male wasp by their entrance to the genital chamber of the female partner. It will also be demonstrated that there is an unexpected yet important behavioral quirk of the deutonymph during the mating of the wasps that is essential to their transmission to the female wasp. The developmental cycle and economy of the mite in the nest of the wasp, the surprising mechanism whereby miteless females and mite-bearing males emerge from the same nest, as well as an hypothesis accounting for the maintenance of the alliance between wasp and mite, will be the subjects of the next paper in this series.

The Genital Acarinarium of the Female Wasp

The broad, flat recess of the ventral genital chamber of the male *Ancistrocerus antilope,* which serves as the principal abode for genitally borne mites in that sex, contrasts markedly with that of the female wasp. The ventral genital chamber of females is strongly concave within, and is but half so long as that of the males, for it is narrowed and markedly shortened by the fans of muscles that insert on approximately half of its anterior extent. Like the proportionately small, concave, ventral genital chambers of most other male and female *Ancistrocerus,* it provides relatively scant surface to deutonymphs. Ordinarily deutonymphs occur within the female ventral genital chamber in small numbers only, and in this respect it corresponds with the *dorsal* genital chamber of the male wasp.

On the other hand, the dorsal genital chamber of female *Ancistrocerus antilope* is well developed and habitually serves as a primary abode or acarinarium for large numbers of deutonymphs (text-fig. 5, p. 156; Tables 2, 3). Tergite seven is more or less domed, being transversely strongly concave within (*i.e.,* swollen externally). The transparent body wall is markedly invaginated anteriorly and above, forming a broad pocket anterior to the dorsal ramus of hemitergite eight (h-8, text-fig. 5). This pocket is shallow, and laterally it is margined by fleshy folds of the body wall. Unlike the ramus of hemitergite eight, that of hemitergite nine (h-9) is interrupted dorsally. The fleshy papilla that bears the anus lies in repose between the dorsal rami of each side of hemitergite nine, the body wall here defining still another shallow pocket.

When a female wasp bears a sizeable load of mites, all, or nearly all, of the deutonymphs are crowded into the dorsal genital pocket anterior to the anal papilla. Here, as also in the ventral genital chamber of the male wasp, the deutonymphs pack themselves into a coherent sheet of mites when in large numbers. Such a sheet of mites generally clings to the body wall between the anterior margin of tergite seven and the posterior edge of the dorsal half of hemitergite eight, or even hemitergite nine, lining the inner surface of tergite seven (see text-fig. 5, and Plate 1, figs. 4, 5). Individual mites seem to spill over laterally and posteriorly from the mat formed by their associates.

Just as small numbers ($\overline{m} < 1$) of deutonymphs may be found in the dorsal genital chamber of some (*ca.* 11%) male wasps, as a rule only a relatively few (from 1–18) mites are to be found in the ventral genital chamber of the female wasp also. Here the likeness between male and female seems to cease, for 60% or more of the deutonymph-bearing females of the subsample possess at least one or a few ($\overline{m}$ 5) mites in the ventral genital chamber. Such deutonymphs lie principally along the length of the ventral medial groove of the interior face of the seventh sternite, in which the valvulae of the sting lie in repose. It is quite possible that these deutonymphs are often forced out of the genital chamber at stinging or oviposition.

The genital chamber of female *Ancistrocerus antilope* differs from that of other *Ancistrocerus* females, such as that of *A. catskill, A. tigris,* or *A. unifasciatus,* by the relatively more generous development of the dorsal genital chamber, rather than by any truly striking morphological distinctions. However, there need be but little doubt that this slight difference represents an evolved modification of considerable importance to the alliance of *A. antilope* with the mite *Ensliniella trisetosa.*

Mating

It by no means proved a simple matter to test the inference (pp. 148–149) that mating would reveal, where experiments had wholly failed, the mechanism of the transfer of deutonymphs from the propodeal to the genital acarinarium of male *Ancistrocerus antilope,* and the cause of the very evident reduction of the mite load with increasing age. For one thing, most female *A. antilope* are fertilized and nesting at the end of August, and generally resist the advances of males with remarkable pugnacity. For another, females used in mating experiments should be reliably free of genitally borne deutonymphs at the onset of a mating test. Yet at that time of year female *A. antilope* are only occasionally (*ca.* 1 in 20 ♀♀) found without deutonymphs in the genital chamber, and more often than not these females are obviously old, and at times of a strikingly lethargic mien. Furthermore the period of etherization, and the extensive manipulation required to determine whether internal mites are truly absent, left the few females otherwise eligible for the test in states of marked debility. No success was therefore had in 1951, although several preliminaries to copulation were witnessed. Trap nests (Cooper 1953) were consequently set in early July of 1952, and from them eight virgin females of the first generation of the year were individually reared in watch glasses for the mating tests. These females were reliably without mites at their exit from the pupal exuvium, and thereafter to the time of mating. Although 40 freshly caught, deutonymph ladened males were paired with these females in the mating tests, only three of the virgin females actually submitted to consummation of the courtship and intromission.

The eight virgin females were separately enclosed in gauze covered vials with individual males. Four were paired only once each in this way, and two of these four females mated. The fifth female mated when enclosed with its second male partner. The remaining three females were paired respectively 6 times, 8 times, and 20 times, and died without actually copulating. Each of these three showed indifference or downright hostility to some of the males with which it was paired, but all submitted to courtship by other males, and details of courtship and of preliminaries were repeatedly verified with them.[7]

The freshly caught males used in the mating experiments were mostly carriers of large, exclusively propodeal loads of deutonymphs, although some had but a relatively small number of propodeally borne deutonymphs and an abundance of mites in the ventral genital chamber (determined after the test). As it later proved, the fact of an earlier mating could safely be inferred for at least those males with genitally borne mites, but the recency of previous mating could not be guessed. Of course it is possible that those pairings in which wasps showed mutual indifference (*v.* records of ♀♀ *D, E* and *G,* footnote 7) were ones in which the males were, for the time at least, spent. Since the prior sexual history of only the female partners is known for these tests, the results regrettably cannot be used to form a certain judgment whether or not virgin female *Ancistrocerus antilope* are refractory to mating, or "coy" (*v.* Richards 1927). Nevertheless the fact that half of the virgin females (namely *B, C, D, E*) immediately showed hostility toward some partners, and since all females (including *F* and *H* which mated at first test) required courting from an initially recalcitrant state, it does seem probable that the female wasp is coy. Since males are almost always the first to emerge from a nest, and since an emerging female has some likelihood of first encountering a brother, deferment through coyness of at least some copulations would confer an element favoring outbreeding within the population.

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[7] If, for each pair mating, courtship be symbolized C, mutual indifference I, hostility H, and actual mating with intromission M, then the 40 tests with the 8 females may be rendered: ♀*A* (C), ♀*B* (CCHHCCCC), ♀*C* (H), ♀*D* (CCHCHCCCIHICICHHCCHC), ♀*E* (CHICHH), ♀*F* (M), ♀*G* (IM), ♀*H* (M).

If the male wasp is not indifferent or hostile to the female, nor in turn is hostilely repulsed by her, he very rapidly mounts the female's dorsum and establishes a firm purchase there. Mounted, the head of the male is at the level of the female's occiput (text-fig. 6, p. 156), and his clypeus and mandibles lie over and hold to the edge of the anterior margin of the pronotum. The tarsi of the forelegs cling to the anterior face of the female's procoxae, or to the upper mesepisternal or epicnemial face of her thorax. The mid-legs are held to the side, or during periods of rest one or the other may encircle the female's waist or petiole. The hind-legs, on the other hand, are enwrapped under the petiole, with the femora and tibiae lying between the posterior face of the propodeum and the anterior face of the second (apparent first) abdominal segment. The pairs of wings of each wasp, longitudinally folded along the pleats characteristic of vespids, are held more or less horizontally and at a 20°–30° angle to each other. The abdomen of the male lies parallel and over that of the female.

The courtship is a complicated and remarkable affair. For a moment the male strokes and rapidly drums the female's antennae with his own. During this process the terminal joint ("hook") of the male's antenna is held out at right angles to the antennal length, and the female usually holds her antennae more or less horizontally, and at an angle of about 120° to one another. The antennal play is complicated, and if there is an overall, detailed pattern, I did not succeed in discerning it. During moments of antennal play, the male may run his tongue between the occiput and pronotum of the female, and it may be wondered whether the sex-limited, postocellar glands of the female's vertex provide the male with secretions at this time.

There is a perfectly evident pattern to a male's attempts to gain intromission, and the cyclic repetition of this pattern comprises most of the courtship. One antenna of the female may be drummed or tapped while the other is stroked, one may be tapped, the other unattended, or both may be stroked or tapped simultaneously or alternately. Thereupon the male curls his abdomen forward under that of the female, exserts his phallus, spreads its parameral lobes wide, stretches mid-legs straight out to each side and at right angles to the body, buzzes for an instant with his wings, and then

both male and female hold their antennae erect as the male snaps (as though by release of a taut spring) his phallus back along the female's sternites to the tip of her abdomen. Here the parameres, digiti and cusps seize the tip of her abdomen, and the phallus is rocked quickly back and forth in a manner seemingly contrived to pry open the genital chamber of the female. During this process the aedeagus is held out of the way, being lifted dorsally from between the parameres.

After a moment the male recurls his abdomen to the other side of the female, and the whole process is again repeated. These events pass rapidly, and between each completed, labored effort to work open the female's genital chamber, the male may or may not pause, stroke, tap and drum with his antennae, lick with his tongue, or rock his body back and forth to each side a few times. If intromission is not achieved after 4–16 of these efforts ($\overline{m} = 8.4 \times$), taking from 20 seconds to 1 minute per complete cycle ($\overline{m} = 38$ secs/cycle), the male thereupon gives up his attempts, and merely rides the female, from time to time indulging in casual antennal play. After such a rest of 4 minutes to an hour or more, and unless the male dismounts or is cast off by the female, the routine is again repeated. Ordinarily each period in which repeated attempts are made to gain intromission has a total duration of 2–10 minutes, with a mean duration of 5.2 minutes. The total time that males devoted to a female before dismounting ranged from 4 minutes to (just) more than 5 hours, with a mean total time of 40 minutes. Excluding the disparate 5 hour period, the adjusted range is from 4–75 minutes, and the adjusted mean is 19.4 minutes. Although males dismounted by the female may immediately attempt to remount and establish purchase again, males that have dismounted of their own initiative remain indifferent or become overtly hostile to their recalcitrant partners. During all the male's attentions and vigorous attempts to copulate, the female may be restive, passive, or increasingly cooperative. A restive female may lie over to one side, cheek to the substratum, or endeavor to fly, or walk about. When the male snaps the phallus back across the female's abdominal sternites, the abdomen of the female may be lifted 20° or more. Some females, of their accord, lift the tip of the abdomen to this position before the phallus is sprung.

If the claspers of the phallus, in twisting, prying, and rocking back and forth at the apex of the female's abdomen, find these segments to be parted, the phallus is speedily inserted in such fashion that the sting is forced out and upward, the two gonostyli or parameral spines of the phallus embracing the ninth tergite of the female between them. The venter of the abdomen of each wasp is rotated nearly 90°, so that, in part, sternite faces sternite (see text-fig. 6, p. 156). Although correlation within the genital conduit is almost certainly *direct* (that is, the dorsal aspect of the aedeagus is contiguous with the dorsum of the vagina [see Lamb 1922]), the genital chambers are in nearly *inverse* correlation. As can be seen in the figure, the terminal sternite of the male wasp rests across the lateral face of the female's 9th tergite; conversely the last sternite of the female abuts against the terminal tergite of the male wasp. In Lamb's (1922) terminology, then, a pair of *Ancistrocerus antilope* assume a *male vertical pose* at intromission, and very likely have *direct correlation* within the genital conduit, but a modified, nearly *inverse correlation* of genital chambers.[8] Finally the *position,* or attitude during copulation and after the point of intromission, is the same as the *pose,* or attitude in courtship. During the period of intromission, which endured 12, 27, and more than 28 minutes in the three cases observed,[9] the male occasionally strokes and taps the female's antennae with his own. The female in turn is passive or restless. She may walk about, attempt to fly, or spends much of her time vigorously cleaning her face with her forelegs.

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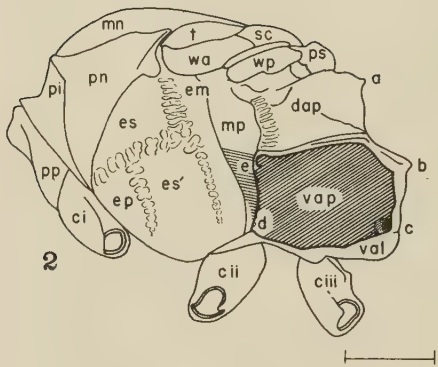
[8] A rereading of Lamb's very interesting and thought-provoking essay suggested that some emphasis should be given to the fact that the *female vertical pose* need not, as Lamb holds, imply that the female is still the active partner in initiating pairing, or indeed that it is active at all. Nor does this pose necessarily involve a simple inversion of the hypopygium. In *Boreus* (Mecoptera) the female is wholly passive, even cataleptic, during the assumption of the female vertical pose, and the correlation of the genital tubes is *inverse* (*v.* Cooper 1940). Assuredly an inverse correlation of genital tubes would seem to involve no special difficulties when the aedeagus is chiefly or wholly fleshy.

[9] In the third case the full duration is not known since the couple was killed at 28 minutes.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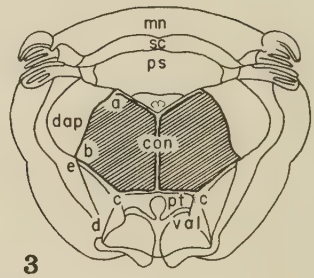
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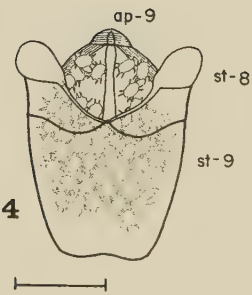
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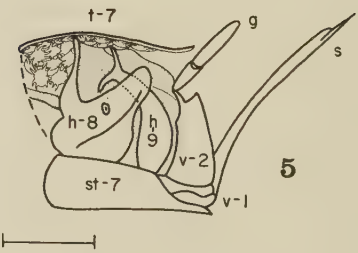
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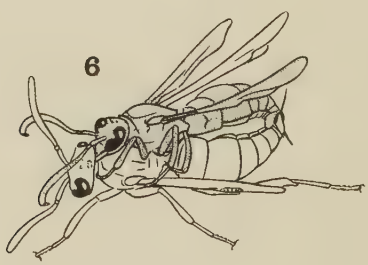

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Figs. 2, 3.—Diagrams of the thorax and propodeum of *Ancistrocerus antilope* (Panzer) in lateral (fig. 2) and posterior (fig. 3) views. Acarinarial sites are indicated by oblique lines; for their description and boundaries, see text. The scale represents 1 mm. Key to abbreviations: a, superior angle of propodeum; b, propodeal angle; c, inferior angle of propodeum; ci-ciii, coxae of legs 1-3; con, concavity of propodeum; dap, dorsal lateral area (superior face) of propodeum; em, mesepimeron; ep, epicnemium; es and es', upper and lower mesepisternal plates; mn, mesonotum; mp, metapleuron; pi, anterior pronotal inflection; pn, pronotum; pp, propleuron; ps, post-scutellum; pt, propodeal tooth; sc, scutellum; t, tegulum; val, valvula; vap, ventral lateral area (inferior face) of propodeum; wa, base of anterior wing; wp, base of posterior wing. *N. B.*, e and d are reference points only; see text.

Fig. 4.—Diagram of the terminal sternites of male *Ancistrocerus antilope* (Panzer). The mites are seen in the acarinarium of the ventral genital chamber; the disarray is not normal, but was brought about by preservation of the male in alcohol. The scale represents 1 mm. Legend: ap-9, spiculum, or median apodeme of sternite-9; st-8, st-9, sternites 8 and 9.

Fig. 5.—Diagram of the terminal abdominal segments of female *Ancistrocerus* antilope (Panzer), the lateral face of tergite-7 having been cut away. The mites are seen in the dorsal genital chamber; the disarray is not normal, but was brought about by preservation of the wasp in alcohol. Compare with figs. 4 and 5 of Plate 1, in which larger numbers of deutonymphs pack the dorsal genital chamber. The scale represents 1 mm. Legend: g, gonostylus or sting palpus; h-8, h-9, hemitergites 8 and 9; s, sting valvulae; st-7, sternite 7; t-7, tergite 7; v-1, v-2, first and second valvifers.

Fig. 6.—Copulating pair of *Ancistrocerus antilope* (Panzer), male stippled. Note the way in which the mandibles of the male are thrust between the occiput and pronotal inflection, and just behind the occipital glands, of the female wasp, the near 90° rotation of the venters of both wasps so that sternite faces sternite, the exserted sting of the female, the manner in which the seventh tergite of the female lies between the parameral spines of the male, and *especially* the portal (blackened) which lies between the united terminalia of male and female and that opens to the genital chambers of the mated wasps. The figure is copied from the notebook sketch of the mating described on p. 161, 162; no mites emerged to the exterior during the copulation.

The Mode of Transfer of Deutonymphs between Acarinaria, and the Mechanism of their Loss from Male Wasps

It came as a surprise that the deutonymphs loading the propodeal acarinaria of male wasps are not actually displaced or mechanically disturbed in any evident manner during the manoeuvres of courtship. In only three instances did propodeal deutonymphs become active and leave their neighbors during the preliminaries to mating. In these cases the few mites that wandered off seemed to do so in an aimless manner, but chiefly on the abdomen of the male. In one of these, two mites crossed over to the female, later settling together in her left propodeal acarinarium.

On the other hand, deutonymphs of the ventral genital chamber of an internally heavily ladened male may in part break ranks and exit from the genital chamber, during exsertion of the phallus, to run about on the outer margins of the male's apical sternite and abdominal tip, or up the abdomen to the thorax. Very likely by accident, for there seems no special goal to the deutonymph's wandering, a few to a dozen or more of these deutonymphs may be transferred to the terminal abdominal segments of the female wasp. Their wanderings there are ordinarily short-lived, for the female wasp seems instantly aware of their presence, and promptly cleans them off by scissoring her hind tibiae against the tip of her abdomen. Any mites that escape this treatment, and remain on the female at the close of a fruitless courtship, may come to reside in her propodeal acarinaria. After several such sterile encounters with a male, one female had acquired some 30 deutonymphs in her right propodeal acarinarium, 0 centrally, 8 in the left propodeal acarinarium, and 0 in the genital acarinarium. Inasmuch as this female had remained in the vial overnight with the deutonymphs that she had scraped off during and immediately after the courtship, most or all of her mite load was very likely contributed by them. As mentioned earlier (see pp. 126–127, 141), free deutonymphs will clamber onto a wasp and load the propodeal acarinaria.

Although the unsuccessful attempt at mating tells little of the mechanism of any major transfer of mites between acarinaria or between wasps, it does make clear a very probable origin for some of the rare and generally small loads of deutonymphs that are

borne by female wasps, as well as a basis for losses of relatively small numbers of deutonymphs from the overall population of mites carried by *Ancistrocerus antilope.*

The courtship that culminates in copulation is quite another matter. Within 2 minutes of intromission, and as though suddenly galvanized to activity, deutonymphs of the propodeal acarinaria of a moderately heavily ladened male broke ranks. Although small numbers moved directly across to the female wasp, the vast majority of deutonymphs streamed down the abdomen of the male to the point of union of the genitalia of the two wasps. Where the genital chambers of male and female wasp interlock at copulation, there is a gap that opens directly to the ventral genital chamber of the male, and to the dorsal genital chamber of the female wasp (text-fig. 6, p. 156). The deutonymphs swarmed into this portal, and during the whole period of intromission they could be seen teeming about, back and forth, between the genital chambers of the two wasps, while smaller numbers of deutonymphs clambered hither-thither over the abdominal tips, remaining for the most part on the abdomen of the male. It was an astonishing sight, and there could be no question at all of the response of the deutonymphs. They responded to some stimulus, they became goal-directed, and they energetically strove to pack themselves into the genital chambers which, during copulation, form a common cavity.

When the male and female broke apart, many fewer deutonymphs remained externally on the female wasp than on the male. All were on her abdomen, and with what seemed frantic concern she succeeded in scraping all but one from her body. There was a fairly large number on the abdomen of the male wasp, and the male also made some effort to clean them off with his hind legs. The deutonymphs on the male, however, were again evidently goal-directed, for they climbed speedily back to the propodeal acarinaria with very little straggling or unoriented wandering.

Before copulation, the total load of the male wasp was 220 deutonymphs (as judged by my count of mites *after* the wasps were killed), and these had been nearly symmetrically distributed among all three propodeal acarinaria. There had been no deutonymphs in the genital chamber of the male before copulation, and the virgin female had been entirely without mites. Twenty-six minutes following separation of the copulating wasps, the balance sheet was drawn thus:

	Number of mites on:	
	♂	♀
Mites located in the acarinarium of the:		
posterior propodeal face	9	0
left propodeal face	12	1
right propodeal face	9	0
dorsal genital chamber	0	69
ventral genital chamber	90	2
TOTAL	120 (+2)	72

In addition there were 2 deutonymphs (= + 2 above) clinging to the left side of the anterior face of the male's apparent abdominal tergit-1, and 26 were creeping on the walls of the vial in which mating had occurred. Almost certainly the two extra-acarinarial deutonymphs would have returned to the propodeal acarinaria of the male. This mating, then, resulted in a minimal loss of deutonymphs from the male's propodeal acarinaria as follows: 41% were translocated to the ventral genital chamber of the male, 32% were transferred to the genital chamber of the female partner, and 12% were simply cast out of the population of mites carried by wasps. Only 0.5% were transferred to the propodeum of the female wasp.

The males of the other two successful copulations at the onset carried only 11 and 2 propodeal deutonymphs respectively, but each had sizeable genital packets of mites. In the first of these matings, once intromission had been achieved, swarms of deutonymphs issued from the genital chamber of the male through the orifice or open port that unites the now common space of the genital chambers with the outside. These deutonymphs did not wander off and about the body of either partner during the 27 minutes of actual copulation, but ran about the surfaces of the terminal segments of both partners, re-entering the genital chamber to be replaced by others from within. The deutonymphs within the common space of the united genital chambers could be seen to be milling about and passing back and forth between male and female sides. Just before the close of copulation there were fewer mites on the abdomens of the wasps, and one-half hour after the wasps had parted the balance was drawn thus:

	Number of mites on:	
	♂	♀
Mites located in the acarinarium of the:		
posterior propodeal face	6	0
left propodeal face	6	0
right propodeal face	9	14
dorsal genital chamber	1	121
ventral genital chamber	66	0
TOTAL	88	135

In addition, some 15 mites were creeping about the wall of the vial.

Before copulation the total load of the male must have been at least 11 propodeal mites + 227 in the genital chamber, or 238 in all. It is worth observing that the genital load in this case is nearly 12% more than the maximum genital load found in any of the 100 censused males of the subsample (*cf.*, p. 134 and Table 3).

Assuredly the propodeal loading of both this male and female at thirty minutes following copulation does not reflect normal events. Under natural conditions wasps almost certainly depart from the site of copulation following cleaning themselves. If this be so, then the entire propodeal load of the female, and half that of the male, is in a sense artefactual. During copulation none of the male's small number of propodeal deutonymphs left their acarinaria, and male and female wasp alike succeeded in completely cleaning their abdomens free of mites. But as wasps seem unable to deal effectively with mites climbing on their mid-legs or wings, and perhaps elsewhere, there is little doubt that the 10 deutonymphs that added to the propodeal load of the male, and all those of the female, climbed onto the wasps after cleaning had been completed.

In view of the above considerations, it is concluded that only 33% of the deutonymphs remained with the male, 51% transferred to the female partner, and again there was a fair loss (16%) of deutonymphs from the population of mites carried by wasps.

During the third copulation the deutonymphs could be seen, through the orifice at the point of union, creeping from the genital chamber of the male to that of the female. No deutonymphs exited to the outer body surface, as in the case just described, no doubt due to the much smaller genital load borne by this male. The two deutonymphs did not budge from the male's propodeal acarinaria.

At 28 minutes after intromission had occurred, the mated pair was dropped into boiling water in an effort to instantly fix, or preserve, them *in copulo*. Though they initially remained together, they regrettably parted at pinning. Since the mites transferred to the female were clearly visible within her genital chamber, it could be estimated that she had received about half of the male's total load, or some 60–70 mites.[10] Presumably no deutonymphs would have been lost from the population of mites following this mating, since none exited to the abdomen from which cleansing may occur. Transfer was solely from the genital chamber of the male to that of the female.

The matings just described include instances in which the male has (a) a large load of propodeal deutonymphs only, (b) a very large load of deutonymphs in the genital chamber, and finally (c) a moderate load of genitally borne deutonymphs. Admittedly there is risk in broadly generalizing from these three cases only, especially since the copulations occurred under certainly abnormal, very restricted conditions that would prevent activities which perhaps occur normally. For example, if mated *Ancistrocerus antilope* usually hang from their support, or fly *in copulo* as Rau (1935) observed a pair of *Monobia quadridens* (Linn.) to do, or the sexes go their separate ways at the close of mating as Jørgensen (1942) has described for a mating of *Symmorphus sinuatus* (Fab.), then they could not have done so in my experiments. Furthermore such close confinement may both hinder courtship, although it did not seem to do so, and prolong the period of intromission. Nevertheless, despite these reservations, there can be no doubt at all that the larger facts concerning the mechanism of transfer of deutonymphs may safely be read from these observations. They are these:

(1) The deutonymph, and not the wasp, makes the transfer, whether it is from the propodeal to the genital acarinaria of the male, or from a male to female wasp.

(2) Only at intromission, during mating of the two wasps, is the opportunity provided for the transfer of deutonymphs from propodeal to genital chamber of the male, or from male to female wasp.

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[10] Since the male and female wasp still preserved the attitudes of their genital parts at copulation, they were not dissected and an actual count was not made.

But mating not only provides the opportunity, it also provides some unanalysed yet necessary stimulus for the propodeally borne deutonymphs.

(3) A tropistic drive is evidently released in the deutonymph by this stimulus, for they quickly break up their packed formations and stream down the abdomen of the male to enter the united genital chambers of the mated pair.

(4) The path of the mites to the genital chamber, and from the genital chamber to the propodeum, is morphologically defined on the wasp by fine recumbent hairs of the abdomen that are reflected posteriorly. Dorsally and laterally, anterior to the propodeal acarinaria, the nearly erect, quite dense hair acts as a fairly effective barrier to anteriorly creeping deutonymphs; such deutonymphs, meeting these erect hairs, ordinarily settle down on the characteristically shagreened, sparsely haired, shining surface of a propodeal acarinarium.

(5) Genitally borne deutonymphs transfer from the genital chamber of the male to that of the female by their own activity. The wasps provide only the physical bridge, and perhaps some stimulus and morphologic guide to the path.

(6) Deutonymphs that are located on the abdomen of a wasp, after copulation, are in peril, for the chance that they will be scraped off is a very good one if the wasp is a female, but perhaps less so if the wasp is male. In this way, and also at courtship, deutonymphs are (almost certainly) permanently lost from the total population of mites that ride adult wasps.

Although these conclusions seem securely drawn, many interesting and important questions remain for answer if a more complete picture is to be had. Among these are the following: Do non-virgin females bearing genital loads of deutonymphs mate? If so, is there an exchange of deutonymphs between the sexes so that those within the genital acarinarium of each sex are of mixed origin following copulation? What deutonymphal transfer occurs in matings of virgin females with males having small genital loads (say 30–50 mites, or less); is the packet of mites partitioned between the sexes, or does the female receive them all? Can a male wholly lacking deutonymphs obtain a genital load from a female with its genital acarinarium full of mites? The answers to these

questions bear importantly on the population dynamics of the mite, and especially on the degree of panmixia (which is probably limited) in *Ensliniella*. Whatever the answers to these questions may be, it is now proven that the mating of the wasp *Ancistrocerus antilope* has become a moment of crisis in the life of the mite *Ensliniella trisetosa,* as well as an essential thread of continuity between successive generations of both the wasp and its mite.

Discussion

No one today knows how complex, how varied, or how widespread the relations of mites with Hymenoptera may be, but there can be no question that some highly diversified, extraordinary, and biologically illuminating alliances with mites are now widely disseminated among aculeate Hymenoptera. Hymenoptera of many families, perhaps most, including tenthredinoid, apocrit and aculeate forms, are sporadically to be found ladened with mites, or subject to their nuisance. Their associations with mites are often apparently no more than as far-ranging transports that have come available to deutonymphs, tritonymphs, or perhaps even adult mites. Orussids that sometimes bear pyemotids (? *Siteroptes*) on abdomen and thorax, and occasional figitids and aulacids ladened with deutonymphs, serve as examples. In other cases, Hymenoptera fall simple prey to indiscriminately entomophagous mites; sawfly and ichneumon larvae that occasionally die from the mass attacks of female *Pyemotes* (= *Pediculoides*) *ventricosus* (Newp.) are cases in point. But these are commonplace encounters with mites suffered by insects generally, and no special interest attends them when the host's role is played by a hymenopteran.

On the other hand the aculeate Hymenoptera seem to have been singled out for special, often bizarre, relationships with mites. Witness, for example, the association of *Antennophorus* with the ant *Lasius* (Wheeler 1910), or of *Dinogamasus* with the carpenter bee *Mesotrichia* (Skaife 1952). In the former case the mite shows very special adaptations for its life with the ant, but the ant seems to have been little affected during its association with the symphile. In the latter case, however, the female bee, and only the female, is curiously adapted to the transport of the mite, having a pouch-like acarinarium deeply invaginated into its second abdominal tergite. The mite lives its whole life with the bee and, as Skaife's

noteworthy study has shown, very probably feeds upon integumentary secretions of larval and pupal *Mesotrichia.* In both these cases the gain to the mite is obvious, and persistence of the alliance is very likely now necessary if the mite is to survive.

But does the ant or bee gain from the association in any way? As in each case the mite takes nutriment or secretions from the hymenopterous host, it would seem to the advantage of the ant and the bee to be rid of the mite. Since the *Antennophorus-Lasius* association is not the rule, in principle the ant could become free of the mite without harm to itself. But the acarinarium of the female bee, and the nearly universal association of female *Mesotrichia* with *Dinogamasus,* suggest that this alliance is no longer a casual affair, and that in the long run the bee needs the mite as fully as the latter does the bee. What the bee's need may be will be discussed elsewhere; suffice it to say that Skaife has convincingly demonstrated Leveque's (1930) suggestion that the mite grooms and cleanses the bee and its nest to be wrong.[11]

Almost certainly the principal factor making for a rich variety of mite-aculeate alliances has been that characteristically aculeate device, the nest, in which so great a part of the life span of the hymenopteran is spent. Protected, generally secure from the weather in both summer and winter, with favorable humidity, with prey or pollen meal, and occupied only by relatively sluggish and helpless larvae and pupae, the aculeate nest is potentially a fertile ecologic domain in which enterprising entomophagous, saprophagous, and even phytophagous, mites may find secluded niches that are nearly or wholly free of competitors. To very small, flightless animals these ecologic niches are accessible and exploitable only if a statistically regular rapport is established with the builder of the nest, namely with the female aculeate. It is not surprising, then, that the principal members of the little known microfauna of aculeate

[11] Leveque (1930, especially 1932) concluded that the mites clean the bees *because* well groomed female bees regularly possess mites, whereas very messy females, matted with pollen, equally regularly do not. Had the relative mean ages of the bees of these two classes been taken into consideration, it would have been difficult to escape the conclusion that young female imagos are initially loaded with mites, old female bees lack them, and hence (as with the male of *Ancistrocerus antilope*) the mite load is dissipated with time. Skaife (1952) has demonstrated that mites initially loading a female *Mesotrichia caffra* (Linn.) are later to be found in the larval cells of her nest.

nests are mites, and that characteristically these mites gain the nest by riding the nesting hymenopteran. Conversely, no surprise need be felt that bethylids, dryinids, and other non-nesting aculeates, are unknown to have regular associations with mites. Finally, it must also be clear that exploitation of this niche must be gentle: a mite or its progeny that starved, mutillated, or killed its aculeate host would leave the new generation of mites forever sealed or buried in a small cell, in a vast limbo, for there could be no return of these mites to the life and nests of the next generation of wasps. Very likely, then, the mites affined with wasps and bees today have descended from ancestors that made slight or only modest demands upon their hosts, or their host's provisions. Assuredly this has been so for the saproglyphid types (in Zachvatkin's sense), such as *Ensliniella, Vidia, Crabrovidia,* and so on.

The widespread occurrence among saproglyphids of hypopal stages, or deutonymphs, must have been a prime factor in the first steps of the growing alliance, for such preadaptation to transport by insects would make exit from the old aculeate nest, and transport to the new one, highly probable. As long as the cycle deutonymph-adult-deutonymph is not longer than the cycle of the host, adult-larva-adult, nor excessively shorter, such mites could develop fairly high-level infestations of an aculeate species that might be maintained indefinitely without necessitating a notable adjustment by either partner. Such, for example, seems to be the state of affairs in the frequent occurrences of *Vidia concellaria* Cooreman on *Cerceris arenaria* Linn. (Cooreman and Crevecoeur 1948), of an unidentified *Vidia*-like ensliniellinе common on a local megachilid bee, of species of *Crabrovidia* on certain *Crabro* (*s.l.*), and so on. The mode or level of infestation must simply guarantee that the frequency of deutonymph-infested female aculeates will not fall, for a period of successive years at least, below some minimal level.

The requirement that female aculeates be infested by deutonymphs, at least in those species where only the female visits and provisions the new nest, is probably reflected in what is perhaps a widespread behavioral quirk of these mites, already inferred by Zachvatkin (1941) and Blüthgen (1953), namely that they must tend to transfer to female insects if initially located on male hosts.

An adaptive behavioral pattern of this sort is not without parallel among other nest parasites of aculeates, for it has been developed in the life cycles of meloid and rhipiphorid beetles, as well as in those of Strepsiptera. The most obvious time and opportunity for such a transfer is at mating, and it is a reasonable guess that such transfers will commonly be found when the matings of infested wasps and bees are studied.

Of all families of Aculeata, the Vespidae promise the greatest rewards and insight to the investigator of such alliances with mites. Very likely, within the subfamily Eumeninae, a whole spectrum of association occurs, from the most casual to the most complex and closely integrated. On the one hand populations of forms such as *Ancistrocerus catskill* (Sauss.) and *A. tigris* (Sauss.), to mention but two, maintain low levels of infestation with mites (*i.e.*, from 2–10%, confidence limits at the 95% level). Whether or not their mites are host-specific, and thus host-dependent, has not been determined, but assuredly the survival of the wasp is independent of the mite. On the other hand there are eumenine forms, such as *Acarozumia amaliae* (Sauss.) (Perkins 1908, Bequaert 1921), certain species of *Nortonia* (Bequaert 1918), *Allodynerus* (*Lionotus*) *delphinalis* (Gir.) and related forms (Vitzthum 1925, Crèvecoeur 1945, Blüthgen 1953), and our numerous *Parancistrocerus* (Bequaert 1925, Bohart 1952), that have recessed acarinarial chambers, or acarinarial pouches deeply invaginated into the propodeum or abdomen. So far as known, the mites harbored in these acarinaria are peculiar to the wasps involved, or shared by closely related wasps. It seems quite possible that in these cases the mite has somehow become as fully necessary to the wasp, as a wasp is to the mite. This need not necessarily be taken to mean that the wasp has truly benefited in any way from its now supposedly enforced alliance with the mite. Indeed, the association may have cost the wasp a drastic loss of its potential for future survival.[12]

Between these extremes are cases such as that of the association of *Monobia quadridens* (Linn.) with a peculiar, pallid mite that is

[12] Once the facts of the life history of *Ensliniella trisetosa* in the nest of *Ancistrocerus antilope* have been described, as they will be in the next paper of this series, a model that can formally account for the origin and maintenance of a mutual dependency will be presented.

frequently to be found in an acarinarium located at the anterior face of the third (apparent second) abdominal tergite. Unlike the cases of *Ancistrocerus catskill* and *A. tigris,* therefore, *Monobia* bears a definite morphologic adaptation well fitted to the mite's needs in transport, yet unlike the cases of *Parancistrocerus,* and the others above, *Monobia* are apparently frequently free of mites.[13] This situation may well be a derived one, and represents a difficult evolutionary problem.

The remarkable transfer of deutonymphs from male to female *Ancistrocerus antilope,* involving as it does passage from the genital chamber of the male to that of the female, has no known parallel in the few cases that have so far been described by other entomologists. Nor is a genital transfer in *Parancistrocerus* likely, to judge from my examination of several hundred *P. pensylvanicus* (Sauss.) and *P. pedestris* (Sauss.). In no case did I find deutonymphs or their remains in the genital chamber of either sex.

Nevertheless genital acarinaria and a genital passage of deutonymphs are not unique to the species *Ancistrocerus antilope.* Recalling that the little known, exceedingly rare *A. spinolae* (Sauss.) is morphologically very similar to *A. antilope,* I examined specimens of *A. spinolae* in the collections of the Museum of Comparative Zoology at Harvard University, of the Academy of Natural Sciences of Philadelphia, and of the United States National Museum. To my immense pleasure, the female of *A. spinolae,* like her taxonomic sister *A. antilope,* carries deutonymphs in the ventral genital chamber, but the propodeal acarinarial areas are always (or nearly always) free of mites. What is more, the deutonymphs that *A. spinolae* carries are of a form close to, or perhaps identical with, *Ensliniella trisetosa* Cooreman. Regrettably the only recorded male of *A. spinolae* (v. Bequaert 1925) appears to have been mislaid or destroyed, and no other seems to have since been found. Nevertheless we may fairly confidently expect male *A. spinolae* to carry deutonymphs in an expanded ventral genital chamber, or

[13] Despite what may appear excessive caution, I wish to point out that even if most *Monobia quadridens* are found to be without mites at capture, it is still possible that all, or nearly all, of the nests of *Monobia* may in fact prove to be infested with this mite. Regrettably, those who have studied the nest of *Monobia quadridens* (*e.g.*, Rau and Rau 1918, Rau 1931, Frost 1944) make no comment as to the presence of mites.

to have propodeal loads of deutonymphs, or, as in *A. antilope,* to carry both propodeal and genital loads of mites. Interestingly, and strengthening this conclusion, an unidentified Korean species of *Ancistrocerus,* reminiscent of both *A. antilope* and *A. spinolae,* also carries packets of mites in a genital acarinarium. Yet the genital acarinarium is very likely not a unique specialization peculiar to certain wasps included in the genus *Ancistrocerus* as now constituted. There are in my collection, for example, a male specimen labelled *Rygchium marginellus* (Fabr.) that has its genital chamber and the interstices of its phallus packed with mites, as well as a few other exotic eumenines that bear genital packets of mites.

It is indeed a notable fact that three closely allied *Ancistrocerus* prove to carry deutonymphs, and in fact carry them in a similar yet very unusual way, namely in the genital chamber. Furthermore, in at least two of these cases the mites in turn are also known to be closely allied. There seem to be other instances of this sort. For example, there are two genera or complexes that are recognized on morphologic grounds, *Allodynerus* and *Parancistrocerus,* in which each included species is a carrier of mites. It is accordingly difficult to avoid the questions that come to mind: Will a combined study of mite-bearing eumenine wasps as a group, and of their mites, disclose clear patterns of affinity now concealed by current taxonomy? Has there been a parallel evolution to grossly similar types on the part of eumenine wasps that had mite-bearing ancestors, and those that came from stocks never affined with mites in any regular manner?

These wasps, it must be pointed out in conclusion, deserve extensive experimental exploitation by biologists interested in population genetics and population problems in general. One hindrance to the study of the population genetics of insects has been the slight success experienced in dealing with natural populations under natural conditions: ordinarily balance sheets cannot be drawn, for at best egg, larval and pupal mortality can be only roughly estimated. Ordinarily the population directly assessed is one of adults only. But the trap nest method can yield virtually all of the information that is needed about non-imaginal stages, and by its use a great deal can also be learned of the adults in rather simple ways. Once sealed by the wasp, the trap nest preserves in entirety the record

of the group of eggs that it contains. Such nests can be taken to the laboratory and the inmates investigated at leisure. Trap nests make it possible to learn exactly what provisions are stored; how rapidly eggs are laid, and how many; what the primary sex ratio is; which zygotes, and how many, die at the egg, larval, prepupal and pupal stages, and what causes them to die; what the incidence of parasitism is, and what the parasites are; what the phenotypic diversity may be within the progeny of a single female; and so forth. Furthermore the proper placing of trap nests allows an estimate of ecologic range, of competitors, and of the intensity of competition, no less the mortality record for the sampled population (*v.* Cooper 1953).

Furthermore the change of stations of the deutonymphs within the population of wasps makes it possible, in *Ancistrocerus antilope* at least, at any time during the flight season, and without killing the wasp, to estimate the relative numbers of unmated and mated males and females, and their percentages of the total population. The mites also provide indisputable evidence that, in some years at least, *A. antilope* may have three generations in one season. In September of 1951 and 1952 for example, the occurrence of males with large propodeal loads of deutonymphs, but empty genital chambers, and of females with fresh liveries but without mites, indicated a new emergence of wasps at that time.

For the enterprising experimental ecologist, population geneticist and evolutionist, then, the eumenine wasps that freely provision trap nests offer a new material for fresh experimental approaches to some of the most interesting and more difficult biologic problems of our time, no less a galaxy of fascinating problems in natural history.

Dedication

This paper is presented to Joseph Charles Bequaert, Louis Agassiz Research Professor at Harvard University, in pleasant anticipation of his forthcoming 69th birthday, and as token of appreciation of his leadership in Natural History.

Acknowledgments

It is a pleasure to record the kindness extended to me during this study by James A. G. Rehn of the Academy of Natural Science of Philadelphia, John Wilcox of the New York State Museum at Albany, and Karl V. Krombein of the United States National Museum, all of whom placed specimens in their custody at my disposal for study. M. Jean Cooreman, of the Institut Royal des Sciences Naturelles de Belgique, obligingly discussed through the mails a number of problems regarding the mite and its taxonomy, and consented to accept the task of erecting a new genus to receive *Ensliniella trisetosa* Coor. Needless to add, the good fortune of appointment to a summer fellowship at the Edmund Niles Huyck Preserve, Rensselaerville, N. Y., made this study possible.

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Explanation of Figures

Plate I

Male (figs. 1-3, 6-7) and female *Ancistrocerus antilope* (Panzer) carrying deutonymphs of *Ensliniella trisetosa* Cooreman. The specimens are in alcohol, and many deutonymphs have loosened from the wasps, with consequent disarray and loss of mites.

Figs. 1-3, mites partially loading the right, posterior, and left propodeal acarinaria of male wasps.

Figs. 4-5, dissections of the genital chamber of female wasps showing packets of deutonymphs in the dorsal genital acarinarium. In both females the deutonymphs extend over hemitergite-8 and posteriorly beyond hemitergite-9.

Figs. 6-7, dissections of the genital chamber of male wasps from the left side (6), and from the dorsal aspect (7), showing deutonymphs located in the ventral genital acarinarium that lies within the 8th and 9th abdominal segments. Fig. 6 portrays a specimen in which the entire genital chamber and phallus have been split sagittally. In fig. 7 the 8th and 9th segments have been rotated, and the tergites, phallus and dorsum of the ventral genital chamber have been stripped away; the deutonymphs are seen clustered on the inner surface of sternite-9. Note that no deutonymphs reside in the visible propodeal acarinaria of either female, or of the male in fig. 6. The male of fig. 7 has a small cluster of deutonymphs in the left propodeal acarinarium, and they can be made out just above the middle tibia.

COOPER—BIOLOGY OF EUMENINE WASPS

ON SOME GERSTAECKER TYPES OF NEOTROPICAL ORTHOPTERA. I. MANTEIDAE

BY JAMES A. G. REHN

Academy of Natural Sciences of Philadelphia

In 1889, in the pages of a paper entitled, "Charakteristik einer Reihe bemerkenswerther Orthopteren,"[1] Dr. Adoph Gerstaecker described eight new genera and forty-three new species of Neotropical Orthoptera, these representing a total of twenty-two genera. Of these species the majority was from Amazonia, and especially the upper Amazon in Brazil and Peru, although several were from Chiriqui in the present Republic of Panama. The species considered represented the superfamilies Mantodea and Acridoidea.

In placing a number of these species Gerstaecker disregarded Scudder's pioneer studies of the seventies based on eastern Peruvian material, and, as was customary at that time, gave but little consideration to Walker's numerous species described from the same general region. It has long been desirable to make a critical analysis of Gerstaecker's genera and species and, where needed, to coordinate his work especially with that of Scudder. Also Gerstaecker's descriptions, while quite detailed as far as color is concerned, are frequently lacking in important structural details, without which the true relationship of some of his species cannot be determined. No figures of the new species accompanied the descriptions.

Some years past the University of Greifswald, in the Museum of which most of the Gerstaecker Orthoptera types were placed, permitted me to study the types of Gerstaecker's West African Blattidae, a detailed report on which, with numerous figures, appeared in due course.[2] Subsequently his types of Neotropical Orthoptera were placed in my hands for similar study. The events of

[1] Mittheil. Naturwiss. Verein Neu-Vorpommern und Rügen, Greifswald, xx, pp. 1-58.

[2] Proc. Acad. Nat. Sci. Phila., LXXXIV, pp. 405-473, pls. 30-33 (1933).

the last decade and a half, with their general disorganization of so many plans and projects, prevented earlier completion of this work, although portions of this restudy have already seen the light in various regional or systematic contributions, and the proper relationship of some of Gerstaecker's species thus have been critically determined and reported. The studies already published in which certain of the Gerstaecker species have been discussed, on the basis of type examination, are as follows:

"The Orthoptera of Costa Rica, Part I.—Mantidae." By James A. G. Rehn. Proc. Acad. Nat. Sci. Phila., LXXXVII, pp. 167-272 (1935). The synonymy of *Acanthops adusta* Gerstaecker under *Metilia brunneri* (Saussure) (pp. 260–261) and of *Acanthops contorta* Gerstaecker under *A. falcataria* (Goeze) (p. 262, footnote 269) was confirmed from type evidence.

"Revision of the Neotropical Euthymiae (Orthoptera, Acrididae, Cyrtacanthacridinae)." By James A. G. Rehn. Proc. Acad. Nat. Sci. Phila., XC, pp. 41-102 (1938). The type of *Rhicnoderma olivaceum,* the genotype of Gerstaecker's genus *Rhicnoderma,* was discussed (p. 51), the synonymy under it of *R. glabra* Bruner was established, and the relationship of the genus determined more definitely than had previously been done.

"A Review of the New World Eumastacinae (Orthoptera, Acrididae). Part II." By James A. G. Rehn and John W. H. Rehn. Proc. Acad. Nat. Sci. Phila., XCIV, pp. 1-88 (1942). The types of Gerstaecker's *Mastax militaris* (p. 73, text-fig. 53, pl. 2, figs. 9 and 11) and *M. plebeja* (p. 78, pl. 1, fig. 6) were redescribed, figured and placed, with other species, in a new genus *Eumastacops.*

"The Upper Amazonian Locust Group Hippacres (Orthoptera, Acrididae, Cyrtacanthacridinae)." By James A. G. Rehn and John W. H. Rehn. Proc. Acad. Nat. Sci. Phila., XCVI, pp. 201-226 (1944). Gerstaecker's genus *Cyphacris* was recharacterized (p. 218), its correct relationship to a previously known genus not mentioned by him was determined, and the type of his *C. decorata* was redescribed and figured (p. 221, text-figs. 9-12, pl. 13, figs. 25-26).

It is now possible to publish further comments on certain of the types concerned, in this way to give greater substance to the work of Gerstaecker, and further to correlate his genera and species with

certain of those described by Scudder in earlier years, the types of which are now contained in the Museum of Comparative Zoology at Cambridge, Massachusetts. Physical comparisons of the respective types have been, and are being, made, and the systematic results thus of warranted permanency.

The synonymy of certain of Gerstaecker's species of Manteidae has already been established in the first of the above-listed correlated studies, but without illustrations of the types or the critical comments here given.

Liturgousinae

Hagiomantis superba (Gerstaecker) Plate II, fig. 3.

1889. *Liturgusa superba* Gerstaecker, Mitth. Naturw. Ver, Neu-Vorpomm und Rügen, Greifswald, xx, p. 53. [♀; Jurimaguas [= Yurimaguas], Peru.]

The unique type is in perfect condition except for the lack of one antenna. The species is correctly interpreted by Giglio -Tos in his study of the family.[3] I am, however, unable to make a critical comparison of *superba* with the genotype *H. ornata* (Stoll), its Guianan counterpart, as no material of Stoll's form is available at this time. Whether the two are really distinct species, or *superba* merely an upper Amazonian subspecies of *ornata* I am not able to determine at this time.

In addition to the type I have examined the following material of the species:

Teffe, Amazonas, Brazil; I, 21, 1920; (H. S. Parish); one female; [A.N.S.P.].

Igarapé de Candelaria (8° 43′ S., 63° 54′ W.), Rio Madeira, Brazil; (E. A. Smith); one female; [A.N.S.P.].

Liturgousa nubeculosa Gerstaecker Plate I, fig. 2.

1889. *Liturgusa nubeculosa* Gerstaecker, Mitth. Naturw. Ver. Neu-Vorpomm. und Rügen, Greifswald, xx, p. 54. [♀; Ega and Fonteboa, Amazonas[, Brazil].]

1915. *L[iturgusa] peruviana* Giglio-Tos, Bull. Soc. Entom. Ital., xlvi, p. 77. [♀; Peru.]

The original material of this species consisted of two females, one from each of the localities given. Of these that from Ega, the

[3] Das Tierreich, lief. 50, pp. 291-292 (1927).

locality standing first, is here selected as the single type. The measurements of the two specimens are as follows, the dimensions of the Ega specimen in each case being given first: length of body, 38.3, 45.2 mm.; length of pronotum, 11, 11.7; greatest width of pronotum, 3.8, 4; length of metazona, 7.8, 8.4; length of tegmen, 21, 23.2; greatest width of tegmen, 7.5, 8.2; length of wing, 15.2, 18.6; length of cephalic femur, 10, 10.7; length of caudal femur, 12.6, 13; length of caudal tarsus, 10+, 11.6; length of proximal article of caudal tarsus, 6.8, 7.6.

Both of the original specimens have been spread and the wings are somewhat damaged in the selected type. The latter also lacks one antennae, a median and a caudal tarsus, and the apex of the other caudal one. The Fonteboa paratype lacks one caudal tibia and tarsus.

The synonymy of Giglio-Tos' *peruviana* is unquestioned and has already been indicated by me.[4] There is no feature in his description which is not seen in the series of *nubeculosa* now before me.

The species is a near relative of Westwood's *L. mesopoda*,[5] which latter may prove to be limited to the Guianas, and of which I have before me a single female from Nouveau Chantier, French Guiana, being one of the five of that sex which were correctly reported by Chopard [6] from St. Laurent du Maroni and Nouveau Chantier.

When *nubeculosa* is compared with the above specimen of *mesopoda* it is seen at once that the former has the pronotum of the shape more usual in the genus, while *mesopoda* has the lateral borders of the same much straighter and subparallel, with the supra-coxal dilation very weakly marked, the granulations of the pronotal surface are almost entirely on the metazona, instead of generally distributed as in *mesopoda*; the tuberculations on the external surface of the cephalic femora are fewer and slightly larger instead of more thickly and generally placed as in *mesopoda*, and similar tubercles are not present on the same face of the cephalic tibiae, as they are in *mesopoda*; the median and caudal femora bear

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[4] Proc. Acad. Nat. Sci. Phila., LXXXVII, p. 198 (1935).

[5] Rev. Insect. Fam. Mantid., p. 30, pl. 13, fig. 10 (1890). [♀; St. Laurent du Maroni, French Guiana.]

[6] Ann. Entom. Soc. France, LXXX, p. 323 (1911).

no tubercles on their dorsal surfaces, while in *mesopoda* these areas are definitely (median pair) or weakly (caudal pair) multituberculate; in *nubeculosa* the marginal field of the tegmina is much less closely, densely and regularly veined by transverse ramulae. In addition the single specimen of *mesopoda* does not show the mediolongitudinal blackish pencilling of the internal face of the cephalic femora seen in all the specimens of *nubeculosa* before me.

In addition to the Gerstaecker material, I have before me the following specimens of *nubeculosa*, which demonstrate the species has a very broad east and west distribution.

Jimenez, Cauca, Colombia, elevation 1600 feet; III, 1907; (M. G. Palmer); one female; [A.N.S.P.].[7]

Obidos, State of Pará, Brazil; VIII, 23, 1919; (H. S. Parish); one female; [A.N.S.P.].

San Esteban, State of Carabobo, Venezuela; X-XI, 1910; (M. A. Carriker); one female; [A.N.S.P.].

Cariaquito, State of Sucre, Venezuela; I, 1911; (Stewardson Brown); one female; [A.N.S.P.].

Of these the Jimenez individual is the largest, measuring: length of body, 42[8] mm.; length of pronotum, 11.6; greatest width of pronotum, 4.2; length of metazona, 8.9; length of tegmen, 26.2; greatest width of tegmen, 8.5; length of cephalic femur, 12.2; length of caudal femur, 13.8; length of caudal tarsus, 13.3; length of proximal article of caudal tarsus, 7.6.

Liturgousa lichenalis Gerstaecker Plate I, fig. 1.

1889. *Liturgusa lichenalis* Gerstaecker, Mitth. Naturw. Ver. Neu-Vorpomm. und Rügen, Greifswald, xx, p. 52. [♀; Jurimaguas [= Yurimaguas], Peru.]

The unique type of this species lacks one antenna and the apex of the left caudal tarsus. Otherwise it is perfect, except that the caudal portion of the pronotum has been slightly crushed, apparently when it was captured.

The species was erroneously synonymized by Giglio-Tos[9] under the slender pronotumed *L. annulipes* (Serville), a species from

[7] Recorded by Hebard (Trans. Amer. Entom. Soc., xlv, p. 134 (1919)) as *L. mesopoda*.

[8] Head deflexed, measurement from occiput and not from buccal region.

[9] Das Tierreich, lief. 50. p. 294 (1927).

which it is very distinct. I have already pointed out the incorrectness of this association.[10] It is instead more nearly related to the stockily built *cayennensis* (Saussure) and *maya* (Saussure and Zehntner), being slightly nearer the former, agreeing in the relatively broad tegmina, the character of the accessory neuration of the same, the somewhat more robust pronotum and cephalic femora and less transverse ultimate tergite (supra-anal plate) of the female. From *cayennensis*, however, *lichenalis* can be distinguished by the less produced trigonal ultimate tergite (supra-anal plate) of the female and more angulately produced caudo-lateral angles of most of the distal abdominal tergites of that sex, a feature not at all evident in *cayennensis*.

The type of *lichenalis* measures as follows: length of body, 28 mm.; length of pronotum, 7.5; greatest width of pronotum, 4; length of metazona, 5; length of tegmen, 19; greatest width of tegmen, 8.4; length of cephalic femur, 8.5; length of caudal femur, 9.3; length of caudal tarsus, 9; length of proximal article of caudal tarsus, 4.7.

In addition to the type of *lichenalis* I have examined a topotypic female, taken at Yurimaguas, Peru, April 20, 1920, by H. S. Parish, and in the Academy Collection. This specimen has the lichenose tegminal pattern similar to that of the type but more recessive and less strongly contrasting, while the subopaque aureate tone of the wings spreads over approximately the cephalic half of the radiate field, the same area in the type being as a whole infumate, while the anterior field has its dully orange color infumately clouded.

Acontiothespinae

Acontiothespis amoenula (Gerstaecker) Plate II, fig. 4.

1889. *Acontista amoenula* Gerstaecker, Mitth. Naturw. Ver. Neu-Vorpomm. und Rügen, Greifswald, xx, p. 51. [♀; Pebas (in error Amazonas), Peru.]

1890. *Acontista semirufa* Westwood, Revisio Insect. Fam. Mantid., p. 45, pl. IX, fig. 2. [♀ (erroneously given as ♂); Ega (or Teffe), Amazonas, Brazil.]

The synonymy of these names, first established by Saussure and Zehntner, is clearly evident after a comparison of Westwood's

[10] Proc. Acad. Nat. Sci. Phila., LXXXVII, p. 199 (1935).

description and figure with Gerstaecker's type. Of the two names Gerstaecker's clearly has priority.[11] Giglio-Tos has endeavored to preserve both names,[12] stating that *semirufa* is larger, the pronotum longer with the dilation more marked and the prozona more narrowed, the tegmina hyaline only toward the apex and the infumate band of the wings narrower than half of the anal area, while the abdomen is said to be brownish instead of ochraceous yellow. The evidence for these statements is not given, and certainly only in part evident with Westwood's description and figure and Gerstaecker's type before me. As to size the range is so small as to be entirely within specific limits, and the dimensions given by him for *amoenula* are less than those of the type of that species and as given by its describer. On the other hand the single comparable measurement given by Westwood for *semirufa*, i.e. pronotal length, is a full millimeter smaller than that given for his species by Giglio-Tos, and in this respect is identical with the type of *amoenula* (vide infra). The pronotum in the type of *amoenula* is in all respects as figured for *semirufa,* while the tegminal hyaline area and the wing color pattern in the type of *amoenula* are essentially as given by Westwood for *semirufa.* The small difference in the width of the infumate alar band is clearly individual as a Surinam specimen shows. The abdominal color difference mentioned has been taken from the original descriptions and can be covered by the method of preparation and drying of the specimens. Fair series of females of other species of the genus now before me show an equal tonal range due to dessication.

The type of *amoenula* shows the following measurements: length of body, 24.5 mm.; length of pronotum, 7; greatest width of

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[11] In endeavoring to determine the priority of these names I make a careful search for evidence as both volumes bear the year 1889 on their title pages and have no other detailed information as to exact issue dates. I found that Westwood's volume was not listed by the Entomological Society of London as an accession until 1890, and was definitely reported by the Entomological Society of France as received on March 12, 1890. Volume XX of the Greifswald Mittheilungen was included in the list of works received by the library of the Isis Society of Dresden during 1889 (see their Sitzungsberichte, 1889, p. 41) and was definitely received by the Royal Scientific Society of Göttingen in February, 1889, the list including it having been published April 21, 1889. In consequence Gerstaecker's names are clearly prior to those of Westwood.

[12] Das Tierreich, lief. 50 pp. 501, 505 (1927).

pronotum, 2.4; length of metazona, 4.5; length of tegmen, 17; greatest width of tegmen, 4.2; length of cephalic femur, 7; length of caudal femur, 6.2.

I have also before me a single female of the present species taken at Zanderij I., Boven Para District, Surinam, April 24, 1927, by Forbes and Babiy, received from Cornell University. This specimen fully agrees with the type except that its colors are slightly brighter and the orange red area of the wings is slightly narrower on the radiate field. There is no question in my mind but that this is merely an individual variation comparable to that seen in the wings of the same sex of *A. cordillerae*.

The nearest relative of *amoenula* is clearly Chopard's *A. gracilis*,[13] a paratype female of which is before me. This species, and this specimen, have already been discussed by me,[14] and the opinion then expressed as to Giglio-Tos' treatment of Chopard's name has been strengthened by further study of the problem.

From *gracilis*, Gerstaecker's *amoenula* can be distinguished in the female sex by the definitely shorter pronotum, which has a more robust metazona, slightly more robust cephalic coxae, and numerous color features, as the uniformly pale instead of heavily infuscate internal surfaces of the cephalic femora, and the presence of a dividing hyaline sector in the wings.

Our knowledge of the distribution of the species is limited to the information here discussed, which shows *amoenula* ranges from Surinam to the Peruvian Amazon. Whether it is also present in the Pará district of Brazil remains to be determined.

Epaphroditinae

Metilia brunnerii (Saussure)

1877. *Metilia brunnerii* Saussure, Mém. Hist. Nat. Mex., IV (Mém. Mex. Mant.), pp. 141, 144. [♀; Surinam.]

1889. *Acanthops adusta* Gerstaecker, Mitth. Naturw. Ver. Neu-Vorpomm. und Rügen, Greifswald, XX, p. 57. [♂; Iquitos, Amazonas (= Amazonian Peru).]

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[13] *A*[*contista*] *gracilis* Chopard, Ann. Entom. Soc. France, LXXX, p. 316, 2 figs. (1911). [♂, ♀; St. Laurent du Maroni and Nouveau Chantier, French Guiana.]

[14] Proc. Acad. Nat. Sci. Phila., LXXXVII, p. 255, footnote 246 (1935).

The synonymy of *Acanthops adusta* was established by me in 1935,[15] with more than a dozen specimens of *brunneri*, including the Gerstaeckerian type, before me.

The spread type is perfect except for the loss of one and the distal portion of the other antenna, of the entire left cephalic tarsus and some damage to the right tegmen and wing. I have already published exact measurements of the type.[16] At the same time the distribution of *brunneri* was summarized and data supplied on variation seen in the series.

Acanthops falcataria (Goeze) Plate II, fig. 5.

1778. *Mantis falcataria* Goeze, Entom. Beytrage, II, p. 36. [Ex Seba, Thesaurus, IV, pl. 76, figs. 1, 2, 3 and 4: ♀; no locality given.]

1889. *Acanthops contorta* Gerstaecker, Mitth. Naturw. Ver. Neu-Vorpomm. und Rügen, Greifswald, XX, p. 56. [♀; Iquitos, Amazonas (= Amazonian Peru).] [17]

The unique type of *contorta* is in perfect condition except for the loss of the antennae, the left cephalic tarsus and the extremity of the left caudal one. It cannot be separated from Guianan and lower Amazonian females,[18] which represent *falcataria* as understood by Chopard, except for a few minor features here mentioned. As to the identity of *falcataria*, it is impossible to say positively on which of several species Goeze's name was based, as Seba's figures, which Goeze named, are too conventionalized to show anything specific. The present insect is clearly that to which Stoll in 1813 applied the name *sinuata*,[19] now regarded as a synonym of the older but more poorly defined *falcataria*.

The type of *contorta* has the falcate apices of the tegmina slightly less elongate and very faintly less falcate than in the Guianan and lower Amazonian females, while the post-median lobate arcuation

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[15] Proc. Acad. Nat. Sci. Phila., LXXXVII, p. 260.

[16] Idem, p. 261.

[17] Synonymy established by Rehn, Proc. Acad. Nat. Sci. Phila., LXXXVII, p. 262, footnote 269 (1935).

[18] These are: Nouveau Chantier, French Guiana; (Coll. La Moult); one female; [A.N.S.P ex Chopard]. Kalacoon, British Guiana; I, 3, 1916; (Beebe); one female; [N. Y. Zool. Soc.]. Pará, Pará, Brazil; (Baker); one female; [A.N.S.P.] (Reported by Rehn in 1916; Trans. Amer. Entom. Soc., XLII, p. 263).

[19] [*Mantis*] *sinuata* Stoll, Natur. Afbeeld. Beschr. Spoken, etc., p. 12 and register p. 77, pl. IV, fig. 14, (1813). [♀; Surinam.]

of the costal margin is slightly less rectangulate and a little more rounded. These differences I feel are purely individual, although extensive series may show there is an Upper Amazonian geographic race with such very minor features consistently developed.

In size the type of *contorta* shows the following dimensions (in millimeters) when compared with a Guianan female.

	Length of body	Length of pronotum	Greatest width of pronotum	Length of metazona	Length of tegmen	Greatest width of tegmen	Length of cephalic femur
♀, Iquitos, type of *contorta*	42.5	13.2	4.8	8.6	31.7	9	13.9
♀, Nouveau Chantier, French Guiana	46.5	15	5.6	9.2	40	12	15.4

Explanation of Figures

Plate I

Fig. 1.—*Liturgousa lichenalis* Gerstaecker. Female (*type*). Yurimaguas, Peru. (X 1½.)

Fig. 2.—*Liturgousa nebulicola* Gerstaecker. Female (*type*). Ega, Amazonas, Brazil. (X 1½.)

Plate II

Fig. 3.—*Hagiomantis superba* (Gerstaecker). Female (*type*). Yurimaguas, Peru. (Natural size.)

Fig. 4.—*Acontiothespis amoenula* (Gerstaecker). Female (*type*). Pebas, Peru. (X 1½.)

Fig. 5.—*Acanthops falcataria* (Goeze). Female (type of *Acanthops contorta* Gerstaecker). Iquitos, Peru. (X 1½.)

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